

# The Structure and Development of Reissner's Fibre and the Sub-commissural Organ.

## Part I.

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With Plates 1 to 5 and 8 Text-figures.

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## I. PREFACE.

IN October, 1907, when working in the Zoological Laboratory of the Imperial College of Science and Technology, I undertook, upon the suggestion of Professor Dendy, an investigation into the structure known as Reissner's fibre. Since January, 1908, the work has been carried on in the Zoological Department at King's College (University of London).

At that time the several papers which had been published some years earlier by Porter E. Sargent, in which he had announced his "optic reflex theory," had attracted considerable attention, and his theory had been accepted by the authors of several text-books, notwithstanding that his results had not received adequate confirmation. In view of the very remarkable character of his observations and his deductions therefrom, confirmation appeared desirable, and accordingly I set out to examine the fibre in a number of vertebrates. From the very outset, however, I found that in several important, and, indeed, fundamental particulars, my observations differed markedly from those recorded by Sargent. I have accordingly refrained from publishing any account of my work until, from an examination of a very large



number of individuals of different species, I should be able to place on a secure foundation results which are so greatly at variance with the "optic reflex theory" of Sargent.

As the result of this investigation, extending now over a period of nearly five years, I am convinced that both in its origin in the brain, and in its ending in the sinus terminalis, the condition of Reissner's fibre is altogether different from the account given of it by Sargent, and I shall hope to succeed in demonstrating that this fibre is not a nerve-tract at all, and that consequently it cannot possibly have the function assigned to it by that author.

The investigation has necessitated the preparation and examination of series of sections of the whole or parts of the central nervous system of between three and four hundred individuals, which have been selected from nearly seventy species. I have also endeavoured to ascertain the function of Reissner's fibre by means of experiments upon living fishes performed at the Laboratory of the Marine Biological Association at Plymouth. The results of these experiments, a short account of which has recently been published ('12), are quite in accord with the suggestion made by Dendy ('09) that the fibre and associated sub-commissural organ form part of an apparatus for automatically regulating the flexure of the body.

The altogether unexpected proportions to which the work has attained have rendered it advisable to publish it in several parts. This, the first part, will be confined mainly to an account of the conditions observed in the Cyclostomes.

The literature list appended does not profess to be complete. It includes only the works referred to in this present part, and the reader is referred to the work of Sargent ('04) for a more complete bibliography of earlier writings which have a bearing, more or less direct, upon this subject.

It is with pleasure that I acknowledge my indebtedness to Professor Dendy, to whom the inception of the work was due, not only for his invaluable advice and criticism during the progress of the work and in the revision of the manuscript,

but also for most kindly undertaking the reading of the proofs. Further, he has placed at my disposal some valuable material, and allowed me the use of his large collection of slides. I wish also to express my thanks to Dr. Allen, Director of the Marine Biological Laboratory at Plymouth, and to his staff, for the facilities afforded me for the collection of material and for the carrying out of experimental work while occupying the British Association's table there.

For assistance in procuring other of the material employed in this research I desire to express my obligations to Professor Meek, Dr. Woodland, and Mr. W. F. Allen, while to Mr. R. W. H. Row my thanks are due for the greater number of the photomicrographs used in illustration, and to Mr. Charles Biddolph for assistance in the preparation of many of the series of sections.

## II. INTRODUCTION.

### (a) Methods and Material.

In the brain and spinal cord of almost every specimen examined Reissner's fibre could be recognised without difficulty. In a few instances only was it apparently absent, and this, practically in every case, in animals which had been preserved entire in fixing fluids of low penetrative power, or where, if the brain-case had been opened, as in some of the larger specimens, there had been insufficient exposure of the brain and spinal cord to the action of the fixing reagents.

In the preservation of such of the material as I was able to obtain in the living condition a number of the commonly employed fixing reagents were tried. Of them all, the aceto-bichromate mixture (Bolles Lee, pp. 49-50), with which I had previously obtained satisfactory results on particularly refractory Teleost material, proved the most generally useful, and was latterly made use of almost exclusively, being found to combine fairly rapid penetrative powers with a good hardening action. With this fluid, too,

there is no risk of overhardening, and the material may be left in it safely for several days, or even weeks, and, if thoroughly washed, is always found to be in good condition for staining. It has, too, the further advantage that small entire specimens left in it for several days usually do not require subsequent decalcification.

Specimens of small size (small ammocœtes, embryo dog-fish, Teleosts up to 30 mm., or even 40 mm. in length, amphibian larvæ, etc.) were, as a rule, plunged whole into the fixing fluid; in the case of larger specimens some dissection was necessary.

Wherever practicable freshly killed material was taken, and the brain partially exposed as rapidly as possible, the entire animal then being plunged into a large quantity of the reagent. Further dissection to complete the exposure of the brain was usually carried on while the specimen was immersed in the fixing fluid.

Such specimens as were sufficiently small were sectioned entire, all risk of damage to the central nervous system being thus avoided. In most cases, however, the length of the central nervous system was too great to admit of the cutting of longitudinal sections through its entirety. In these, the brain (or head) with a considerable portion of the spinal cord behind it, and also the terminal piece of the spinal cord, were removed, but, before the spinal cord was severed, the exposed portions of the central nervous system were allowed to become thoroughly penetrated and fixed. The severance of the spinal cord might generally be safely performed, where aceto-bichromate was the reagent employed, after the lapse of from half an hour to one hour, according to the size of the specimen.

By the adoption of this precaution the characteristic recoil of the fibre, with the resulting tangle of its free ends, which has been remarked by several observers (Sargent, '04, Nicholls, '12), was generally prevented, and the fibre was preserved in its natural relations. In one or two instances, however, it was found that Reissner's fibre had, notwith-

standing, suffered accidental breakage prior to, or during, fixation.

In the case of some of the larger animals, in order to ensure thorough penetration it was found necessary to remove part of the brain on one side. This was cut away with a razor, but only after partial hardening, in order to lessen the risk of crushing together the parts of the brain and the consequent disturbance or displacement of the fibre. Where practicable, however, the brain was preserved entire, the removal of part being found to be necessary principally in the case of mammalian brains.

Many different stains were employed, Reissner's fibre being stained strongly by several of these. It is brought out especially well after fixation in aceto-bichromate by heavily staining in bulk in Grenacher's borax-carmines, followed, upon the slide, by picro-indigo-carmines. This latter stain was prepared by mixing one part of a saturated solution of picric acid in 70 per cent. alcohol with two parts of a saturated solution of indigo-carmines in 70 per cent. alcohol. Sections immersed for about five minutes in this solution become considerably over-stained. This excess of stain is got rid of by washing in a number of changes of 70 per cent. alcohol till all trace of free picric acid is removed. (If the washing be not thorough the residual picric acid begins to crystallise out in a few days.) Sections treated in this way usually show axis-cylinders stained red, with medullary sheaths green, while Reissner's fibre appears of a dull purple tint. Nerve-cells stain variously, the nuclei of all being particularly well brought out, while the cytoplasm, in most cases, is only lightly stained; in the "Dachkern" cells, however, the cytoplasm becomes well stained, and takes on a reddish or purplish tint. Blood-corpuscles are stained green.

If the washing in 70 per cent. alcohol has been prolonged, Reissner's fibre fades to a pale blue or blue-green colour, and connective tissues appear bright blue.

Another stain which has given me good results is iron-braziliin used as described by Hickson ('01). Some especially

satisfactory results have been obtained by the use of this stain with brains of *Petromyzon* which had been fixed in aceto-bichromate, the nerve-fibres being wonderfully defined. It is, indeed, particularly useful for material where the fibres are non-medullated.

Various hæmatoxylin stains were also tried, and generally served to bring out Reissner's fibre well. Ehrlich's acid-hæmatoxylin stains the fibre strongly, and Heidenhain's iron-hæmatoxylin upon aceto-bichromate material in particular yields very satisfactory results. A modification of Weigert's method, suggested by C. J. Herrick, was tried upon material fixed in aceto-bichromate as well as upon material fixed in Flemming's stronger fluid and in Zenker's fluid; in every case Reissner's fibre was found to take the stain strongly, but was readily decolorised by any of the several decolorising fluids commonly employed.

As a test for elastin, both Unna's orcein stain and Weigert's elastin stain, which were brought to my notice by Professor Dixon, were tried upon the fibre in the spinal cord of the frog, and with both reagents the fibre became stained, but lightly.

The methylene-blue stain recommended by Ramsey ('01) was employed upon both Teleost and Elasmobranch brains. It was observed that Reissner's fibre took up the stain quite well, but unfortunately the stain appears to be transient.

The rapid method of Golgi was tried upon Elasmobranch material (*Raia*, *Scyllium*), and although quite satisfactory general impregnations were obtained, I found, as apparently all previous observers have done, that Reissner's fibre invariably fails to become impregnated. This fact has been explained by Sargent as probably due to the presence of much non-dialisable colloid material in the cerebro-spinal fluid which surrounds the fibre, which was supposed to interfere with the action of the fixing fluid. Accordingly, in preparing some Selachian material for this method, I removed about one third of the brain by a longitudinal vertical cut, thus partly exposing the ventricles and allowing the cerebro-spinal fluid to drain away, but Reissner's fibre did not even

then become impregnated. In *Raia*, in particular, it was noted that the cells of the "Dachkern" and of the sub-commissural organ were also unimpregnated, and, for that reason, were conspicuous as yellowish patches upon the almost black background.

A modification of the method of Bielschowski, suggested by Stewart Paton ('07), was tried upon embryo *Scyllium canicula*, and upon a small teleost (*Esox*) brain. In the case of both, successful impregnations were obtained, nerve-fibres being picked out in a deep blue-black, while unimpregnated tissue takes on a soft grey tint. Reissner's fibre appeared homogeneous, and showed no indication of the coloration to be observed in neuro-fibrillæ, but took on the pale grey colour. The cells of the "Dachkern" and the giant cells of the cord became heavily impregnated, the network of neuro-fibrillæ within some of these latter (in embryo *Scyllium*) being wonderfully defined.

The material examined includes:

CYCLOSTOMI.—*Petromyzon fluviatilis*, *Ichthyomyzon* (*Entosphenus*) *tridentatus* (ammocetes only), *Geotria australis*, *Myxine glutinosa*, *Bdellostoma cirrhatum*, *B. (Polistotrema) stouti*.

ELASMOBRANCHII.—*Chimæra* (*Hydrolagus*) *colliciei*; *Scyllium canicula*, *Raia* (three species), *Rhina squatinata*.

GANOIDEI.—*Lepidosteus osseus* (larvæ).

TELEOSTEI.—Some twenty or more species of the genera *Esox*, *Anguilla*, *Phoxinus*, *Umbra*, *Gobius*, *Blenius*, *Gasterosteus*, *Syngnathus*, *Agonus*, *Cottus*, *Trigla*, *Mugil*, *Rhombus*, *Gadus*, *Labrus*, *Lophius*, *Box*, etc.

AMPHIBIA.—Both adults and larvæ of *Amblystoma* sp., *Salamandra* (two species), *Molge* (two species), *Rana* (two species), and adults only of *Hyla* sp., *Bufo vulgaris*, and *Bombinator igneus*.

REPTILIA.—Two different species of *Gecko*, *Lacerta*



(three species), *Anguis fragilis*, *Pygopus* sp., *Hinulia* sp., *Tropidonotus natrix*, *Emys* sp., *Testudo stellata*, *Sphenodon punctatus* (adult and embryonic).

AVES.—*Gallus domesticus* and *Columba livia*.

MAMMALIA.—*Talpa europæa*, *Erinaceus europæus*, *Mus musculus*, *Microtus arvensis*, *Lepus euniculus*, *Cavia cobaya*, *Felis domestica* (?), *Anthropopithecus*, and *Homo*.

### (b) Historical Review.

So very complete a survey of the work of the earlier investigators who have noticed Reissner's fibre and related structures has been given by Sargent ('04) that it will be necessary for me here to do little more than consider the more recent papers which refer to this subject, most of which have appeared since Sargent's preliminary paper ('00).

It is now a little more than fifty years since Reissner ('60) announced his discovery of the fibre which bears his name. He described it as a fine cylindrical rod lying freely in the *canalis centralis* of the spinal cord in *Petromyzon*, but he did not ascertain either its origin or ending. He believed it to be a pre-formed structure of a nervous nature.

For nearly forty years after its discovery the fibre remained strangely neglected, and of the comparatively few observers who mention its occurrence the greater number saw it only in the *canalis centralis* of the spinal cord, and appear to have agreed with Stieda ('68, '73) that the structure was an artifact resulting from the coagulation of the cerebro-spinal fluid under the action of certain fixing reagents. Sanders ('94) deserves notice as being the first observer to trace the fibre forwards (in *Myxine*) into the cavity of the mid-brain, and backwards into the *sinus terminalis*. Mayser ('82), with whose work Sanders appears to have been unacquainted, had previously found the fibre in the fourth ventricle of Teleosts.

A new era in the study of Reissner's fibre may be said to

have commenced with the work of Studnička, who, in 1899, announced that he had observed the fibre in a large number of forms. His description, however, relates principally to Petromyzon. He discovered the posterior end of the fibre in a tangled condition somewhat similar to that described by Sanders in Myxine. He expressed the opinion that it was a pre-formed structure, and stated that he found it to be homogeneous, affording no evidence of internal structure. He concluded that it was non-nervous, and probably produced as a secretion of the ependymal epithelium of the canalis centralis. He failed, however, to observe its connection anteriorly with the sub-commissural organ (although, in Petromyzon, he succeeded in following it forward to a point immediately beneath the posterior commissure), and he supposed, erroneously, that the anterior end of the fibre was free and possessed of the power of growing forward.

Six months later there appeared the first of Sargent's preliminary papers. In this paper ('00) he states (p. 41) that "the course of Reissner's fibre through the ventricles to its termination anteriorly has been most thoroughly studied in Teleosts, where it has been followed continuously in Cynoscion, Pomatomus, Morone, Amia and Salvelinus. The fibre has been followed to its termination in the torus also in Raja, Lepidosteus, Necturus, Alligator, Scelopoteris, garter-snake, and less completely in many other species including the mouse and pigeon." (The spaced type is mine.)

It will be sufficient comment upon this statement to recall the fact that the torus longitudinalis is a structure peculiar to the brain of bony fishes, as was shown by Rabl-Ruckhard long since ('84). What Sargent supposed to be the torus longitudinalis, and labels as such in his text-fig. 1, is evidently the posterior commissure.

Describing the course of Reissner's fibre he says (op. cit., p. 42): "Passing along the median fissure of the torus for one half to two-thirds its length and close to its surface (figs. 8, 9), the fibre passes beneath the membrane which



covers the torus and enters the brain substance (fig. 10). In Cynoscion and Salvelinus the fibre, after passing beneath the membrane, may be followed for  $100\mu$  or more before it breaks up." The "membrane" here referred to, in the light of his text-fig. 1, is indubitably that well-defined tract of highly modified ependymal epithelium beneath the posterior commissure for which the name "sub-commissural organ" has been recently suggested (Dendy and Nicholls, '10).

Sargent further seems to have confused the cavity of the mid-brain with the third ventricle, for he says (p. 39): "As already stated, Reissner's fibre extends through the whole length of the *canalis centralis* of the cord and continues cephalad through the fourth and third ventricles to the anterior end of the optic lobes."

In an appendix to this paper he controverts Studnička's ('99) statements (published six months earlier), and reaffirms his own opinion that Reissner's fibre is a pre-formed structure of a nervous nature.

His conclusions were criticised by Kalberlah ('00) in the same year. This author figures Reissner's fibre in a transverse section of the spinal cord of an embryo of *Acanthias*, and from a study of the condition of the fibre in that embryo he comes to the conclusion that it is an artifact. It is quite possible that what he describes as "*eine ganze Kollektion solcher Fadenquerschnitte*" was simply a tangled mass of fibre, which might easily present such an appearance in transverse section.<sup>1</sup>

Although he actually quotes the sentence from Sargent's paper in which that author refers to the posterior commissure under the name "torus," Kalberlah appears not to have noticed either this or other errors in Sargent's work, to which I have here called attention. Sargent subsequently ('04, p. 135) dismissed Kalberlah's criticism as valueless, remarking that that author had probably himself not seen

<sup>1</sup> I have seen appearances precisely similar to that figured by Kalberlah in sections of the spinal cord of the mouse in which a tangled heap of Reissner's fibre was cut through.

Reissner's fibre because in embryos of *Acanthias* at that age the fibre is not developed.<sup>1</sup>

In this year another paper containing a reference to Reissner's fibre was published by Studnička ('00). Replying to Sargent's criticism of his former work, he remarks that that author's statements require confirmation, and further, that he himself found it very difficult to reconcile the idea of the fibre being a nervous structure with his own observations upon its relations to the *Ventriculus terminalis*.

This paper is also noteworthy in that it contains the earliest careful figures of the modified ependymal epithelium of the sub-commissural organ (in the lamprey and dogfish). In his text the author states that he was unable to determine the function of this epithelium, and he does not appear in the least to have realised its connection with Reissner's fibre.

In the following April Sargent ('01) published a second preliminary paper, dealing this time with the development of the fibre, which, he said (*op. cit.*, p. 445), "has been studied in about twenty different species, and has been more or less completely worked out in representatives of all the chief groups of vertebrates." His descriptions, however, relate only to Cyclostomes, Ganoids and Selachians, in which he claimed to have discovered "axons" which, growing out from numerous conspicuous nerve-cells (the "Dachkern" of Rohon) in the tectum mesencephali, emerged into the aqueductus sylvii either immediately (*Amia* and *Petromyzon marinus* [?]), or after passing forward in the brain-tissue to the anterior end of the tectum (Selachians), these axons uniting in both cases in the aqueductus Sylvii to form Reissner's fibre. Referring to the condition in Selachians he says ('01, p. 448): "Where Reissner's fibre leaves the brain tissue the membrane covering of the roof of the ventricle is continued in a cone-like projection surrounding the fibre

<sup>1</sup> Kalberlah, so far as I can find, nowhere states either the age or the size of the embryo in question. I, myself, find the fibre developed in the closely related *Scyllium canicula* at a very early stage, and Sargent also records its existence early in development in *Mustelus*.

(fig. 9).” This “cone-like projection” is obviously the posterior end of the sub-commissural organ (cf. text-fig. 2, A, B), and this constitutes his only reference in this paper to this organ.

Sargent apparently still continues in this paper to confuse the *aqueductus Sylvii* with the third ventricle, for he says (p. 448): “In the adult *Petromyzon* Reissner’s fibre passes through the *canalis centralis* and the fourth ventricle, from which it enters the brain-tissue of the basal portion of the cerebrum, and passing through this emerges into the third ventricle. Here it breaks up into several trunks and continues forward to the anterior portion of the ventricle, where, after further division, it enters the tectum.” The “basal portion of the cerebrum,” too, is somewhat vague, but Sargent means apparently the postero-ventral part of the optic lobes, and perhaps also of the cerebellum.

Sargent further describes (’01) in the *sinus terminalis* of *Amia*, *Raja erinacea* and *Petromyzon marinus*, free “posterior canal cells,” which, he states, send forward “axons” to meet the backwardly growing Reissner’s fibre, and says (p. 447): “The fibre, then, is a nerve-tract composed of axons running in opposite directions, both cephalad and caudad. The development of this apparatus as outlined for *Amia* is typical for all vertebrates” (my spaced type).

It is in this paper that Sargent, upon what appears to me to be altogether unsatisfactory and insufficient evidence, first puts forward the optic reflex theory, which he formulates as follows (p. 450): “The apparatus which is the subject of this paper forms, I believe, a short circuit between the visual organs and the musculature, and has for its function the transmission of motor reflexes arising from optical stimuli.” His text-fig. A (p. 449) offers a diagrammatic representation of the structure of this “optic reflex apparatus,” but he wholly omits, so far as I can find, to make clear in what way he supposes the alleged axons of the “posterior canal-cells” to be related to the cells of the “Dachkern” or other brain centre.

Sargent states also ('01, p. 451) that "in those species which are totally blind no trace of this apparatus is to be found"—an erroneous statement that has since found its way into several text-books, notwithstanding that, so long ago as 1894, Sanders had mentioned the existence of a particularly well-developed Reissner's fibre in *Myxine*, his discovery being confirmed by Studnička in 1899.

In the latter part of the same paper Sargent gives an account of certain experiments performed upon living sharks, the operation consisting in breaking Reissner's fibre in the fourth ventricle. He states that he observed that "those sharks in which the fibre had been broken showed a slowness in response to optical stimuli," indicated by an inability to turn quickly to avoid obstacles interposed suddenly in their paths. This is construed as evidence that the breaking of Reissner's fibre had interrupted the conduction of optical stimuli by the "short-circuit" path constituted by that fibre. I have pointed out elsewhere ('12) that the evidence afforded by these and other experiments is susceptible of another and much simpler explanation in accordance with Dendy's suggestion ('09), to which I shall have to refer shortly.

Later in the same year Houser ('01) published an account of the neurons and the supporting elements of the Selachian brain, his descriptions being based upon the study of adult *Mustelus*. In this memoir he repeatedly states that he found Reissner's fibre arising as the product of the coalescence of paired fibre-tracts, the constituent fibres of which were the axons of the cells of the "Dachkern," or roof nucleus.

This account of the fibre in *Mustelus* agrees closely with the condition in Selachians as at that time described by Sargent from a study of the embryo of *Raja*, but differs in an all-important particular from the account of the fibre in *Mustelus* and Selachians generally as given subsequently by Sargent (1904), when the fibre was (correctly) described as continuing forwards beneath the posterior commissure.

Houser apparently did not notice (as, indeed, extraordinary as it may appear, no subsequent observer seems to have done)

the startling mistakes in the earlier of the two papers by Sargent, with whose work he appears so entirely in agreement.

In 1901, Cole and Johnstone ('01) drew attention to the occurrence of Reissner's fibre in the *canalis centralis* of *Plenronectes*, and appear to have accepted Sargent's theory without question.

Dendy, early in 1902, unaware that it had been previously described or figured, directed attention to the sub-commissural organ, which he spoke of as a "pair of ciliated grooves." He noted the occurrence, in the ammocœtes of *Petromyzon* and *Geotria*, of a pair of conspicuous grooves lined by long columnar epithelium, the free border of which was beset with short cilia. These grooves were described as beginning at the posterior limit of the habenular ganglia, and extending backwards beneath the posterior commissure to the hinder end of that structure. He suggested that these grooves were concerned in promoting the circulation of the cerebro-spinal fluid.

Kölliker ('02) announced that he had observed Reissner's fibre in members of several different classes of vertebrates, and admitted that it must be accepted as a pre-formed structure to be found in all classes of vertebrates from the birds downwards. He figured the fibre in transverse section in the spinal cord of *Protens* and *Siredon*, and called attention to the widely divergent views upon the nature of the fibre which had recently been expressed by Studnička, Sargent and Kalberlah.

In 1903 there appeared a short paper by Sargent ('03) dealing with the *ependymal groove* (sub-commissural organ). He stated that this serves merely as an attachment plate or anchorage for Reissner's fibre, and omitted all reference to Dendy's paper ('02). He remarked that this structure, while present in all vertebrates, is conspicuous in *Cyclostomes*, *Selachians* and *reptiles*, less prominent in *Teleosts*, *birds* and *amphibia*, and inconspicuous in *mammals*. As has since been shown (Dendy and Nicholls, '10), the last part of this statement (if we except the *Primates*) is entirely erroneous.

In the same year still another work by Sargent appeared ('03A), dealing primarily with the torus longitudinalis, which he this time correctly identified. In this he gives a full historical survey and a description of the condition of this organ in a number of Teleosts. He points out the several errors into which different observers have fallen in attempting to homologise this structure, peculiar to Teleosts, with various parts in the brains of other vertebrates, but appears completely to overlook the fact that he himself had confused the torus longitudinalis with the posterior commissure! He accepts Rabi-Ruckhard's ('84) disproof of the earlier theory that the torus is the homologue of the fornix of higher vertebrates, but denies, rightly enough, that the latter author is correct in supposing that it is homologous with the sub-commissural organ ("ependymal thickening"), pointing out that in Teleosts both of these structures co-exist.

Sargent himself, however, falls into fresh error, as I believe, in stating that the torus is the homologue of the "Dachkern" or roof-nucleus of other vertebrate classes. He claims that he has succeeded in tracing from the cells of the torus three separate fibre-tracts strictly homologous with the three fibre-tracts which he had already traced from the "Dachkern" in Selachians.

I cannot believe that this suggested homology can be correct and, on the contrary, I shall bring forward evidence later in this paper to show that the "Dachkern" nucleus is also present in some Teleosts, and is perfectly distinct from the torus.

In 1904 Sargent published what must be regarded as his principal paper ('04) upon Reissner's fibre, in which he collected and amplified the results announced in his earlier works.

In a footnote (p. 153) he refers to Dendy's ('02) description of the "ciliated grooves" in the brain of the ammocœtes of *Petromyzon* and *Geotria*. He represents that author as stating that the cilia of the grooves are longer than those



occurring on the general ventricular (ependymal) epithelium, whereas what Dendy said was really precisely the opposite. He then goes on to say—"I believe that there are no cilia in the grooves." I shall show later that the grooves are abundantly ciliated.

He, again and more emphatically, on the strength apparently of an examination of a single series of sections through the tail of *Petromyzon marinus*, controverts ('04, p. 160) the account given by Studnička ('99) of the ending of the fibre posteriorly in *Petromyzon* and *Myxine*, and appears to be wholly unaware of Studnička's reply ('00) to his earlier criticism. From his own account and figure ('04, Pl. I, fig. 8) it is evident that Sargent himself had not seen the actual termination of the fibre in the sinus terminalis of the adult lamprey.

In this paper, also, he institutes a comparison between Reissner's fibre and the large (Dachkern) cells from which he says it arises, and the giant fibres and cells of *Amphioxus* and *Chaetopoda* (p. 158), and concludes—"It is possible . . . that Reissner's fibre and the cells which give rise to it are represented by elements in the invertebrate nervous system."

To avoid repetition it will be desirable to postpone a more detailed criticism of Sargent's general results, and also of those of Houser, until after I have given a general account of what I believe to be the true relationships of the parts concerned. Certain other more special criticisms will follow the description of each class.

At the end of his memoir Sargent announced that a second part, dealing with the higher vertebrates, was already well advanced (June, 1904), and would, it was hoped, appear in about a year. This has not yet been published, but in the interval that has since elapsed several references to this subject have appeared in the works of other authors.

Kolmer ('05), in an elaborate paper on the spinal cord of *Ammonoetes*, published in the following year, records the finding of Reissner's fibre in the *canalis centralis* of that

animal, but states that, although he was able to follow it forwards into the cavity of the mid-brain, he could determine neither its origin nor its ending. He disagrees with Sargent as to its nervous nature, and inclines rather towards Studnička's view of its origin and character. In his summary he states (p. 209): "Der Centralkanal enthält konstant den Achsenfaden (Reissner'sche Faden). Es ist sicher kein nervösen Gebilde, wahrscheinlich ein Sekretionsprodukt der Ependymzellen."

In the same year Sargent's theory was accorded a place in vol. ii of Sedgwick's 'Text-Book of Zoology' ('05), where it is stated (p. 195) that Reissner's fibre "consists of a bundle of nerve-fibres and communicates with the tissue of the spinal cord throughout its length. It appears to be absent in blind fishes."

Dendy, in 1907, described and figured the fibre in *Geotria australis*, calling attention to its relation to the sub-commissural organ (ependymal groove). He suggested a possible connection with the pineal eye, a view which he has since abandoned, and, while accepting Sargent's theory as to the nature and function of the fibre, said (p. 15): "I find it difficult to believe that such a remarkable and well-developed structure as the ependymal groove should be required solely for the function which Sargent assigns to it."

In the same year (1907) Sargent's work obtained notice in several text-books. Johnston ('07, p. 148) put forward the optic reflex theory with a certain reserve, but, so far as I can find, his work contains no reference to the sub-commissural organ! Sherrington ('07) apparently accepted the optic reflex theory freely, and in the English edition of Weidersheim's text-book ('07) it also finds a place, though only in a footnote.

In 1908 I announced in 'Nature' ('08) the presence of Reissner's fibre in the frog, and called attention to its relation to the sub-commissural organ in that animal.<sup>1</sup>

<sup>1</sup> I have since found that the fibre had previously been seen in the *canalis centralis* of *Rana* by Stieda ('70), although he did not refer to it by name, and considered it to be an artifact.



In March of the same year, Ayers ('08) described the occurrence of "ventricular fibres in Myxinoids." His descriptions, though somewhat vague, appear to relate to Reissner's fibre, and to confirm, to a large extent, the account of that structure as given in 1894 for Myxine by Sanders, of whose work, as, indeed, of the existence of this fibre in other vertebrates, Ayers seems, however, to have been wholly unaware.

Edinger ('08), who some year earlier had given a very diagrammatic figure of the sub-commissural organ of Scyllium, which he considered to be of a secretory nature, is, I believe, the only recent worker to adhere to Stieda's view that Reissner's fibre is to be looked upon merely as an artifact.

In the same year Horsley ('08) recorded the existence of the fibre in Primates, finding it present in two species of *Macacus*. He mentioned certain experiments, performed by himself and Dr. McNalty, and stated that division of Reissner's fibre was not followed by that degeneration of the distal portion which is characteristic of severed nerves, and he expressed the opinion that Sherrington had been premature in accepting Sargent's theory, lacking, as it did, adequate confirmation.

During 1908-1909 Favaro ('08, '09) referred several times to Reissner's fibre. He summarizes Studnička's work and briefly mentions Sargent's "optic reflex theory," concerning which he offers no opinion. He refers also to Ayers' paper, and reproduces a diagram from Kolmer's work in which Reissner's fibre is shown.

In 1909 Dendy ('09) further announced the occurrence of Reissner's fibre in the cat and the tuatara. He altogether repudiated his former acceptance of Sargent's theory, and put forward an entirely new suggestion as to the function of the fibre and the related sub-commissural organ, pointing out that the fibre may quite possibly play merely a mechanical part in automatically regulating flexure of the body, its variations in tension acting as stimuli upon the cells of the sub-commissural organ to which it is attached.

At the same time I myself ('09) published further evidence of the remarkable elasticity of this fibre, its behaviour in the case of specimens of *Bufo* and *Petromyzon* being instanced. I stated definitely that the fibre was not a nerve-tract, and that the suggestion put forward by Dendy as to its function was quite in accordance with the facts so far as they were then known.

In the following year, in a joint paper (Dendy and Nicholls '10), we showed reason for believing that Reissner's fibre, while present almost, if not quite, without exception in the vertebrate series from Cyclostomes to Primates, may prove to be absent in man. We proposed the name "sub-commissural organ" for the "ependymal groove" with which the anterior end of Reissner's fibre is connected, and pointed out that this organ, far from being "inconspicuous in mammals" as Sargent asserted, is in reality a very conspicuous structure in the lower members of this group (mouse, cat). It is, however, less conspicuous in the chimpanzee, and, while well developed in the fœtal human subject, has become reduced to a mere vestige (the "mesocœlic recess") in the adult man.

Still more recently, Dendy (1910), in an account of the pineal organs and adjacent parts of the brain of the tuatara, has given a short account of Reissner's fibre and the sub-commissural organ in that animal.

In the present year ('12) I have given a short description of the condition of Reissner's fibre in the sinus terminalis of several Elasmobranchs, and described certain experimental work carried out by me upon living fish in an attempt to ascertain its function.

(c) General Introductory Account of the Actual Relations of Reissner's fibre and the Sub-commissural Organ.

As is well known, one of the most constant features—I might almost say the most constant feature—in the roof of the brain of all vertebrates is that tract of transversely coursing

nerve-fibres situate at the junction of the fore- and mid-brain. This tract, which is known as the posterior commissure, is by most authors considered as belonging to the mid-brain, of which it is said to mark the anterior boundary. It makes its appearance in development at an extremely early stage, in that downfolding of the roof (the *plica meso-prosencephalica*<sup>1</sup>) which separates the first brain vesicle from the second. Arising at the same time, or perhaps even earlier in development, is another equally constant but little-known structure, the "sub-commissural organ." This is a conspicuous, longitudinal, paired tract of epithelium, produced by a modification of the ependymal epithelium of the brain ventricle on either side of the mid-dorsal line beneath the meso-prosencephalic fold. The ordinary, almost cubical cells of the ependymal epithelium become in this region enormously elongated and fibre-like. Their nuclei mostly pass inward towards the end remote from the brain ventricle, and the whole structure bears a striking resemblance to the epithelium of a sense-organ. From the inner (deeper) end of the cells neuroglial fibres pass, which, collecting into bundles, radiate towards the *membrana limitans externa* on the upper surface of the brain. The ventricular ends of the cells are beset with short cilia.

In the adult, in almost every case, the ependymal epithelium of the sub-commissural organ passes gradually, in the infundibular recess, into the more typical epithelium of the epiphysial stalk.

The paired nature of this sub-commissural organ remains apparent throughout life in certain forms (e.g. *Petromyzonidae*), but in the greater number of cases there is a confluence of the two tracts along their mesial borders, so that the structure takes on the form of a median plate of columnar cells, and under such circumstances may retain traces of its originally paired character only at its anterior and posterior ends. The shape of this plate is variously

<sup>1</sup> *Plica meso-thalamencephalica* would seem to be a better term for this fold.—A.D.

modified in the different classes of vertebrates, being dependent upon the size and relations of the structures of the mid-brain immediately adjacent. Thus, among the forms that I have examined, the sub-commissural organ appears, in transverse section, as a decidedly horse-shoe-shaped structure in Selachians, reptiles and many mammals (Pl. I, figs. 2, 3, 6, 8, *s.c.o.*), in birds it is strongly arched (Pl. I, fig. 7), and in amphibians (Pl. I, fig. 5) perhaps somewhat less markedly curved, while in many Teleosts it persists merely as a flattened median plate which shows scarcely any trace of its original paired character (Pl. I, fig. 4).

The shape of the sub-commissural organ may be still further modified by transverse folding. In some cases, too, this tract of specialised epithelium extends around the posterior border of the posterior commissure on to the dorsal (posterior) surface of that structure, and may even line a small median anterior extension of the optocœl (the mesocœlic recess) directly above (behind) the posterior commissure (Text-figs. 2, B, and 3, A, *m.r.*).

In man, as was pointed out by Dendy and Nicholls ('10), the mesocœlic recess is the sole vestige of this apparatus. It is connected, in foetal life, with a typical sub-commissural organ, which lies perfectly normally beneath the posterior commissure and bears distinct evidence of its paired origin, but it appears subsequently to lose its connection with the general cavity of the iter, and that part of the sub-commissural organ which lies beneath the posterior commissure altogether disappears.

Between the cilia of the sub-commissural organ are found slender fibrillæ which are distinguishable from the ordinary cilia simply by their greater length. These collect together to form delicate strands which unite to constitute Reissner's fibre. In longitudinal section of the typical brain (compare Text-fig. 5) the fibre is thus to be made out arising well forward from near the anterior border of the sub-commissural organ in the infra-pineal recess. It there lies closely against the surface of the sub-commissural organ near the middle line,

and continues to receive fresh accessions of strands of united fibrillæ along the entire length of the posterior commissure, until it passes caudally from the hinder border of that structure. Thence it stretches as a taut thread lengthwise through the mesocel, usually coming to lie close against the ventral surface of the rhombo-mesencephalic fold. Upon this surface there is almost invariably a median longitudinal groove, which I have termed the "isthmic canal" (Text-fig. 5, *i.c.*). This appears to become deeper with age. It is lined by an ependymal epithelium that differs from the general ventricular investment, the cells being more elongated and staining very strongly. In this groove the fibre lies freely, and, so far as my observations go, never becomes embedded in the brain-tissue (as has been asserted). The isthmic canal is usually deepest at its anterior end, becoming continually more shallow posteriorly till it fades out, and Reissner's fibre, emerging from its hinder end, may be readily traced backwards through the fourth ventricle as a tightly stretched thread which enters the *canalis centralis* of the spinal cord.

The ependymal cells which line the *canalis centralis* are furnished somewhat sparsely with short cilia. Here and there, however, at comparatively short intervals, slightly longer cilia may be made out, which appear to be attached to Reissner's fibre (compare fig. 56). It is, of course, extremely difficult, if not impossible, to determine with absolute certainty that these cilia are not simply lying in contact with the fibre or even glued to it by a coagulum of cerebro-spinal fluid. An examination of a very large number of sections, however, leads me to believe that many, at any rate, of them are indeed actually fused with Reissner's fibre and probably form an integral part of it. Whether, however, they are quite short cilia fused to the fibre only by their tips and serving merely as supports and stays for it, or whether they are of a similar character to the long cilia-like processes of the cells of the sub-commissural organ, I am quite unable to determine, but I suspect that they are of this latter class, and that they

probably take an important part in the growth of the fibre, and may extend backwards in it for an appreciable distance. The fibre extends along the entire length of the *canalis centralis*, maintaining a practically uniform thickness in this part of its course, although, perhaps, diminishing slightly in diameter near its posterior end.

Towards the hinder end of the body the spinal cord undergoes a considerable diminution in size, and tapers off into the delicate *filum terminale*. This becomes a simple epithelial tube, and may, in some fishes, pass beyond the enclosing vertebral canal, to lie unprotected, except for its meninges, just beneath the skin. At its actual extremity the *filum terminale* becomes somewhat dilated, and contains an ovoid enlargement of the *canalis centralis* which is known as the *sinus (ventriculus) terminalis* (fig. 40, *s.t.*). The *sinus terminalis* is, however, only incompletely surrounded by the enlargement of the end of the *filum terminale*, for at about the middle of the *sinus* the *ependymal* as well as the nervous elements of the cord disappear, so that the *canalis centralis* actually opens by a wide aperture, the "terminal neural pore," into a lymph-space that is morphologically continuous with the perineural spaces. The posterior wall of the *sinus terminalis* is thus formed only by the fibrous sheath of the spinal cord, which appears to consist of united *pia* and *dura mater*. From the *canalis centralis* Reissner's fibre passes through the terminal neural pore, behind which point in many cases, if not in all, it expands into a conical "terminal plug" (fig. 51, *t.p.*), which passes into, and blends with, the connective tissue of the meningeal portion of the wall of the *sinus terminalis*.

The actual fibre is an extremely tenuous thread, whose normal diameter in the adult condition in the greater number of species which I have examined is between one and three micra. In well-hardened material it is almost always distinctly brittle,<sup>1</sup> but in life or in the fresh state in recently

<sup>1</sup> In a single case (*Geotria*) the fibre appears to have retained, to a great extent, its flexibility even in Canada balsam.



killed material it must possess a remarkable degree of elasticity. It would appear to exist in life under considerable tension, and, being subject to continually varying strain with every alteration of the position of the long axis of the body, it must be exceedingly liable to accidental breakage. In such an event, or in the case of artificial section in the fresh condition, the elasticity of the fibre brings about a sharp recoil of the broken ends to form large masses or snarls, as shown, for example, in fig. 19. Even when partially fixed by reagents, however, the resilience of the fibre is such that it will still contract if severed. Under these circumstances the retraction appears to be a comparatively gradual one, and the fibre will then be found twisted into a more or less regular spiral (fig. 16), which is often extraordinarily reminiscent of the retracted stalk of a *Vorticella*. Even where the recoil has been an abrupt one and a large knotted mass has formed, a careful examination practically always discovers the existence of such a spiral winding of the fibre (figs. 15, 19). These knots thus have the character of tangled heaps such as would result from the continued twisting in one direction of one end of a thin elastic thread of which the other end is held fast. In every such case there is a marked decrease in length, and an accompanying and very considerable increase in the diameter of the fibre.

Seen in transverse section, Reissner's fibre seems to show a very thin outer sheath investing an apparently homogeneous central core which possesses a very high refractivity. I believe that this thin dark encircling rim is nothing but an optical effect consequent upon the difference of refractivity of the fibre and that of the surrounding medium. That it is a medullary sheath of myelin, as Sargent declares ('04, p. 145), I can find no reason for believing.

According to that author the central part of the fibre shows, in transverse section, a punctate appearance, which he interprets as the effect of the cut ends of the constituent axis cylinders ('04, p. 146). As stated above, I find no trace of any such structure, and if the fibre is, as I believe, the result

of the coalescence of hypertrophied cilia, the fusion is so intimate that the whole fibre has a homogeneous glassy appearance. In favour, moreover, of such a view of the nature of the fibre is the extraordinary rapidity with which it disintegrates at death. It is practically useless to examine material for Reissner's fibre if that material has been dead for an hour or so before fixation, and further, even in material which has been fixed at death, but which is of sufficient size to prevent speedy penetration, or even in small material where a slowly penetrating fluid has been employed, it is rare to find the fibre preserved. In such cases the general ependymal cilia, too, have almost invariably disappeared.

Apart, then, from the doubtful existence of a delicate investing sheath, I have been unable to demonstrate any internal structure in Reissner's fibre, even with the aid of very high powers of the microscope. It seems certain, nevertheless, in view of the constancy of the mode of recoil which the fibre exhibits, that some very definite internal structure must exist.

An explanation may perhaps lie in the manner of development and growth of the fibre. It may well be that when, in early development, the fibre (arising from fused sub-commissural fibrillæ) grows backwards to enter the *canalis centralis*, it is at once joined by similar fibrillæ or cilia from the ependymal cells, which, overlying the earlier formed structure, continue its backward growth. These, in their turn, would be continually covered by fresh accessions, and the entire fibre would resemble a species of "hay-rope." If the whole of these fibrillæ have a slight spiral growth the manner of recoil of the fibre formed by their union would be easily understandable. Even the retention, to a certain extent, of their individuality by the fibrillæ might in itself be sufficient for the spiral retraction. In all such cases of recoil, however, the fibre has torn itself free from its attachments.

I have already suggested that accidental breakage of Reissner's fibre may occur not infrequently, perhaps, in life, and I have obtained a considerable amount of evidence of



the occurrence of this phenomenon in Cyclostomes and fishes. It will be obvious that the sudden recoil of the broken ends which normally occurs, and which results in the formation of a large coiled knot, must be of use<sup>1</sup> in checking the further retraction of the broken fibre, for this knot blocks the comparatively small lumen of the *canalis centralis*, and, presumably, enables the fibre to establish a temporary hold until regenerative processes shall have restored its connection with the wall of the *sinus terminalis*. That regeneration does occur I have ample evidence to show (cf. Nicholls, '12). The large percentage of cases in which the fibre is found broken and recoiled may be due to the exceptionally strenuous exertions of the animals in their efforts to avoid capture causing the fibre to snap.

#### (d) Critical Discussion of the Views of Sargent and Houser.

Before passing on to a detailed account of Reissner's fibre and the sub-commissural organ in the several vertebrate groups, it will be necessary to discuss certain general statements made by Sargent, some of these being said to be confirmed by Houser.

To the former author, and, though perhaps in a lesser degree, to Studnička, is due the credit of having established the fact of the pre-formed nature of the fibre. Sargent further demonstrated the constancy of its relation to the anterior part of the roof of the mid-brain, but, unfortunately, the mistakes in his earlier papers ('00, '01) (especially those consequent upon his failure, at that time, to recognise the posterior commissure, which, as I have shown above, he supposed to be the *torus longitudinalis*), have coloured all his later work, detracting greatly from its value; for, although subsequently both posterior commissure and *torus longitudinalis* were correctly identified ('03, '04), and the

<sup>1</sup> We have an analogy in the formation of a blood-clot operating to close a severed blood-vessel and so to check further blood-flow.

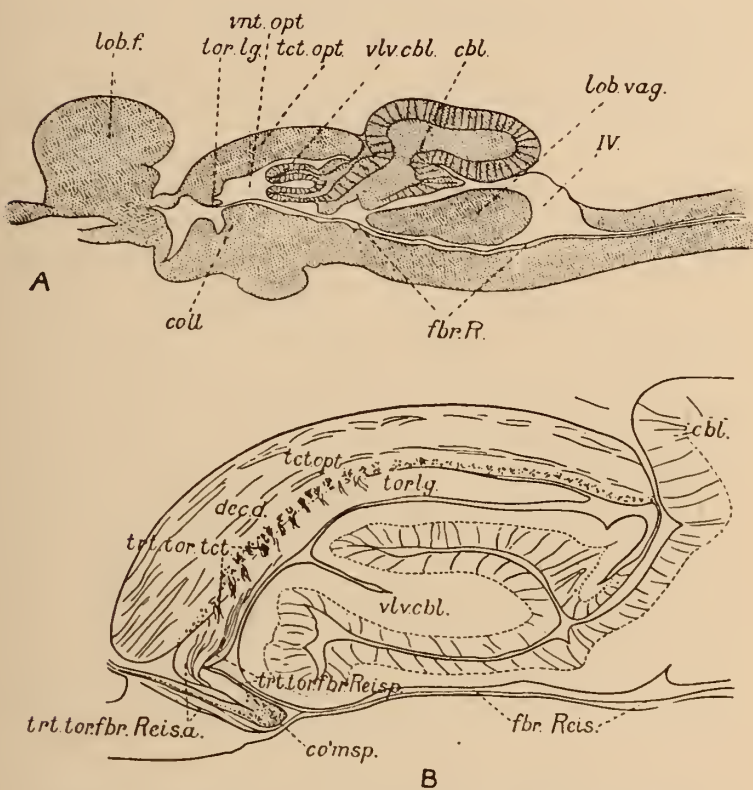
sub-commissural organ (ependymal groove) described in some detail ('03A), Sargent still clung ('04) to the idea that, at any rate in part, Reissner's fibre is traceable directly into the torus, notwithstanding that his original description of such relation of the fibre to the torus was based upon an erroneous identification of this structure. It is clear from his descriptions and also from his text-figure ('00), making allowance for the mistaken identification of the parts concerned, that Sargent actually saw Reissner's fibre lying in its proper position as a single thread below the posterior commissure (termed by him "*torus longitudinalis*") for one half to two thirds of the length of that structure, and then breaking up to join the sub-commissural organ ("the membrane which covers the torus"). In these earlier descriptions he nowhere suggests a division of the fibre into two main branches.

In his last paper, however, he shows the fibre composed of two main factors—(1) an anterior branch which lies beneath the posterior commissure and which is indisputably the fibre originally described by him as solely constituting Reissner's fibre, and (2) a posterior branch which was not indicated in any way in either of his preliminary papers ('00, '01), but which is now stated to pass above (posterior to) the posterior commissure, and is described as emerging into the mesocoel directly from the *torus longitudinalis*. This posterior branch is said to be composed of numerous axons, derived, in Teleosts, from the cells of the torus, which he therefore homologises with the "*Daehkern*," from the cells of which he derives the constituents of the posterior branch in other types.

Sargent does not, however, call attention to this marked discrepancy between his later account and that previously given, and, in the absence of any definite statement to the contrary, the reader is naturally led to suppose that the posterior branch described in 1904 as directly related to the torus is identical with the entire fibre erroneously described in the preliminary paper ('00) as having the same

relations. To render intelligible this somewhat involved matter, I have reproduced in Text-fig. 1 two of Sargent's figures, one (A) being taken from his preliminary paper,

TEXT-FIG. 1.



An exact reproduction of two of Sargent's figures to show the difference between his earlier ('00) and later ('04) accounts of Reissner's fibre and its relations to structures in the mid-brain. The first (A) is taken from his earlier paper ('00) and shows the course of Reissner's fibre correctly, but the posterior commissure is identified (erroneously) as the torus longitudinalis (*tor. lg.*). In B, taken from his latest work ('04), the posterior commissure (*co'msp.*) and torus longitudinalis (*tor. lg.*) are correctly identified, but a second branch of Reissner's fibre has been added, to which the description originally given of the piece ventral to the posterior commissure is now made to apply.

and representing a sagittal section through the brain of a teleost, *Cynoscion regale* ('00, p. 39, fig. 1), the other (E) from his latest paper, representing a similar section through the brain of another teleost, *Pomatomus saltatrix* ('04, p. 209, fig. 1). The brains of both of these fishes had been studied by him when the preliminary paper was written, where it was said of Reissner's fibre ('00, p. 41) that—"its course is the same in all except in so far as it is dependent on the size and relations of the ventricles and other parts of the brain, which differ in different species."

According to my own observations there never is a posterior branch connected with either the torus or the "Dachkern" such as Sargent describes, and one is forced to the conclusion that the introduction of this branch in the later paper (where its course and relations are described in terms practically the same as those applied erroneously to the entire fibre in the first instance) has been due to his neglect to put right the original mistake in identifying the posterior commissure as the torus.

This impression may be a mistaken one, but it is of the utmost importance to emphasise the non-existence of the posterior branch, as it is upon its alleged presence that Sargent's statements as to the connection of Reissner's fibre with the cells of the torus and the "Dachkern" and the consequent homologising of these two structures principally depend.

The anterior branch, which, so far as my own observations go, alone exists, and which, as explained above, was alone figured and described by Sargent in his preliminary paper, is, therefore, in his later work, necessarily described as having (in forms other than Teleosts) quite different relations.

In Teleosts it is traced into the torus longitudinalis by a somewhat devious path through the "Schaltstück" (pars intercalatus) and the posterior commissure, the adoption of such a route being explained by Sargent as due to the early development of the cells of the optic reflex apparatus, which "send their axons into the ventricle from the median plane of the roof (Pl. 7, fig. 47; Pl. 8, figs. 55, 56, 58, *fas.*

*Reis.*) even before the posterior commissure has developed. In the later development the fibres of the posterior commissure, in making their way across from the opposite sides, pass posterior to these axons. Such a pre-posterior commissural tract—the *tractus toro-fibræ Reissneris anterior*—is found only in Teleosts" ('04, pp. 198-199).

Almost all his figures ('04), however, not only for Teleosts but also for Cyclostomes and Elasmobranchs, show Reissner's fibre arising, either principally or entirely, from a point far forward beneath the posterior commissure. In explanation of this condition Sargent suggests that in these forms the anterior branch is probably derived from fibres which issue from cells in the habenular ganglia, and he attempts to explain, too, in this way, the occurrence of the fibre in blind animals (e.g. *Myxine*, *Amblyopsis*, '04, p. 206). In this manner also he would account for the presence in developing *Squalus* of a definite Reissner's fibre, which, he says, "has been traced forward under the *Schaltstück*" in embryos in which the "*Dachkern*" has not yet developed.

I shall show subsequently, when describing the development of the fibre in embryo *Amblystoma*, that the early stages of the development of the fibre are to be seen when neither habenular ganglia nor "*Dachkern*" are distinguishable. In these early embryos, however, the elements of the sub-commissural organ are already well defined, and it is from the ependymal epithelial cells of this sub-commissural organ that the numerous fine fibrillæ, which join up to constitute the fibre, have their origin, all of these fibrillæ arising posterior to the developing epiphysis, and remote, therefore, from the habenular ganglia. I shall also point out that the fibre arises far forward beneath the posterior commissure not only in *Amblystoma* but in all vertebrates, amongst which, in no single instance, do I find the fibre arising either wholly or in part from any point morphologically posterior to the posterior commissure, notwithstanding that in many forms (*Amphibia*, reptiles and birds) a well-developed "*Dachkern*" is present, which should



contribute a considerable branch if Sargent's account were correct.

Sargent devotes some space ('01, '04) to the consideration of the physiology of the "optic reflex apparatus," and gives an account of certain experiments performed by him upon living sharks. He says ('04, p. 231) that "these experiments, though incomplete, show clearly, I believe, that when Reissner's fibre is severed the power to respond quickly to optical stimuli is lost," which, even if it were established, is not at all the same thing as proof that the slowness of response said to have been observed is due either wholly or partly to the retardation of an optical stimulus.

He goes on to compute ('04, p. 240), from theoretical considerations, that the saving of time effected in the transmission of an optical stimulus along the "short-circuit" path afforded by Reissner's fibre would probably amount to at least  $0.016 + x$  seconds (where  $x$  is the delay in one cell-body), or approximately a saving of less than one fiftieth of a second, which is surely an insignificant result for such an elaborate and special apparatus.

In his earlier paper ('01) Sargent had denied the existence of the fibre in blind animals, and stated (*op. cit.*, p. 451) that "experiments are now in progress to determine the effect of artificial extirpation of the eye on this apparatus." The value of such experiments is obvious if, as Sargent believed, the fibre were absent in blind animals, and it would be of considerable interest to know what results were obtained, but in none of Sargent's later works is there any further reference to these experiments, and, as shown above, Sargent had subsequently to admit the existence of a fibre of Reissner in some blind animals, although, as already noted, he endeavoured to explain it away as being probably a case of the fibre functioning solely as an olfactory reflex apparatus.

In discussing the work of Houser, or rather that part of it which relates to Reissner's fibre, it is necessary first to consider to what extent his conclusions may have been influenced

by those of Sargent's works which had at that time been recently published. It must accordingly be borne in mind that in April, 1901, when the second of Sargent's preliminary papers appeared, that author had not apparently attempted to retrieve the mistakes consequent on his initial errors of identification. It is clear, too, from Sargent's descriptions ('01, p. 447-448) and figure (pl. 2, fig. 9) of the condition of Reissner's fibre in Elasmobranchs (as studied by him in very young *Raia erinacea*), that he had not at that time discovered how very far forward the fibre really extends beneath the posterior commissure, which structure, indeed, with its related sub-commissural organ (ependymal groove), he did not, even then, so much as mention.

Into practically identical errors both of omission and of commission, Houser, as I shall proceed to show, also fell. Indeed, it would appear that upon this subject Houser has blindly followed the first lead given by Sargent, while Sargent himself, when giving in his last paper ('04) an account that differs essentially in certain important details from his earlier accounts, yet claims ('04, p. 164) that "Houser . . . has fully confirmed my results as set forth in my preliminary papers"!

Although describing, in Reissner's fibre and its alleged cellular connections in the brain, a structure hitherto undescribed in adult Selachians, Houser failed to give any illustration which would enable his readers to gather clearly at precisely what point "the well-marked tract" of fibres "emerges from the mid-brain roof to penetrate the aqueduct, of Sylvius as the fibre of Reissner" (op. cit., p. 130). Indeed, in none of his numerous figures does he represent Reissner's fibre at all, and the absence, in particular, of any illustration showing precisely where he believes Reissner's fibre to emerge from the mid-brain substance into the aqueduct of Sylvius is the more to be regretted on account of the vagueness of his descriptions.

As is well known, the posterior commissure is included by many authors (Edinger, '08, Johnston, '07) in the mid-brain,

while by others (Burekhardt, '95, Studnička, '05) it is considered as part of the dience-phalon, and as, so far as I can find, Houser nowhere even mentions the posterior commissure, I am totally unable to decide what exactly that author regards as the "anterior limit of the mid-brain," but it seems probable that in this particular his account was intended to agree closely with the account given by Sargent of the origin of the fibre in Raia. The latter author had represented the fibre as emerging wholly behind the posterior commissure.

Of the cells of the "Dachkern," whose axons were supposed to unite to form Reissner's fibre, Sargent had said ('01, p. 447): "The cells are multipolar, giving off several processes in addition to the large axon, which is  $2\mu$  to  $3\mu$  in diameter," and "The axons pass dorsad and laterad from their cells, turning either cephalad or caudad" (my spaced type). Houser, more explicit, stated (op. cit., p. 129) that the axons from those of the cells in the anterior region of the tectum opticum pass cephalad to form Reissner's fibre, while those from the more posterior cells run caudad into the cerebellum. Neither he nor Sargent explained how such a very large number of these axons (in young Raia, according to Sargent, there are three or four hundred "Dachkern" cells with axons from two to three micra in diameter) could possibly become compressed into Reissner's fibre, which has, according to the later account of Sargent ('04, p. 147), even in the adult only a diameter of 6.7 micra. Sargent, however, at a subsequent period, discriminated between finer axons running cephalad to constitute Reissner's fibre and coarse neurites passing posteriorly to the cerebellum, and, ignoring his own earlier statements, dissented from Houser's account, remarking ('04, p. 177): "I believe that each cell sends an axon anteriorly, and also a cerebellar neurite posteriorly."

It is clear, moreover, from figures in Sargent's later work ('04) that he admits the existence in Raia, Mustelus and other Selachians of a relatively considerable part of Reissner's fibre (the anterior branch) unrelated to the "Dachkern." This runs forwards well beyond the point where the alleged fibre-tracts



were supposed to emerge. These latter, therefore (which had constituted the whole of the fibre in *Raia* as originally described by Sargent, and in *Mustelus* according to Houser), could form but a fraction of the entire fibre, so that the difficulty of accommodating these several fibre-tracts within the compass of a single thread whose diameter is little more than that of a coarse nerve-fibre is increased rather than diminished.

The condition of the adult *Mustelus* described by Sargent ('04) thus differs essentially from the condition that this author had previously ('01) figured and described for *Raia*, yet Houser, in the meanwhile ('01), had claimed to have found the fibre in the adult *Mustelus* in precisely that condition which Sargent had described for *Raia*.

Again, Sargent records that "the exact method by which the fascicles enter the ventricle and form Reissner's fibre has been difficult to make out in *Raia*, the connections having been broken away in all my series of sections" ('04, p. 169). He further admits ('04, p. 173) that in *Mustelus*, too, "near the upper limit of the ependymal groove the fibres are lost, but apparently they pass between the ependymal cells into the groove," and "a direct connection between the fibre-tracts described and Reissner's fibre has not been observed in this species." Thus it would appear that Sargent never actually saw in Elasmobranchs that emergence of the constituent axons "between the ependymal cells" which both he and Houser so confidently describe. That Houser, likewise, did not see this "emergence" of these "fibre-tracts" is probable, for in this connection it is not without significance that Houser altogether omits (just as Sargent before him had done) all mention of the posterior commissure, and entirely overlooks the sub-commissural organ (ependymal groove), to which Sargent had not at that time directed attention, although the latter author afterwards described this structure and considered it to be developed as an anchorage and support for Reissner's fibre. This oversight on the part of Houser is the more astounding seeing that he devotes a considerable part

of his paper to an account of the supporting elements (ependyma and neuroglia) in the various regions of the brain, and that it happens that the sub-commissural organ reaches nearly, if not quite, its maximum development in Selachians (see Text-figs. 2, A, B, and 3, A, and figs. 2, 3). That any observer, especially one professing to make a study of supporting elements, could have seen the emergence of the constituent "axons" or "fibre-tracts" (so-called) of Reissner's fibre into the mesocoel, and yet have failed to notice this extraordinarily developed ependymal epithelium is almost incredible.<sup>1</sup>

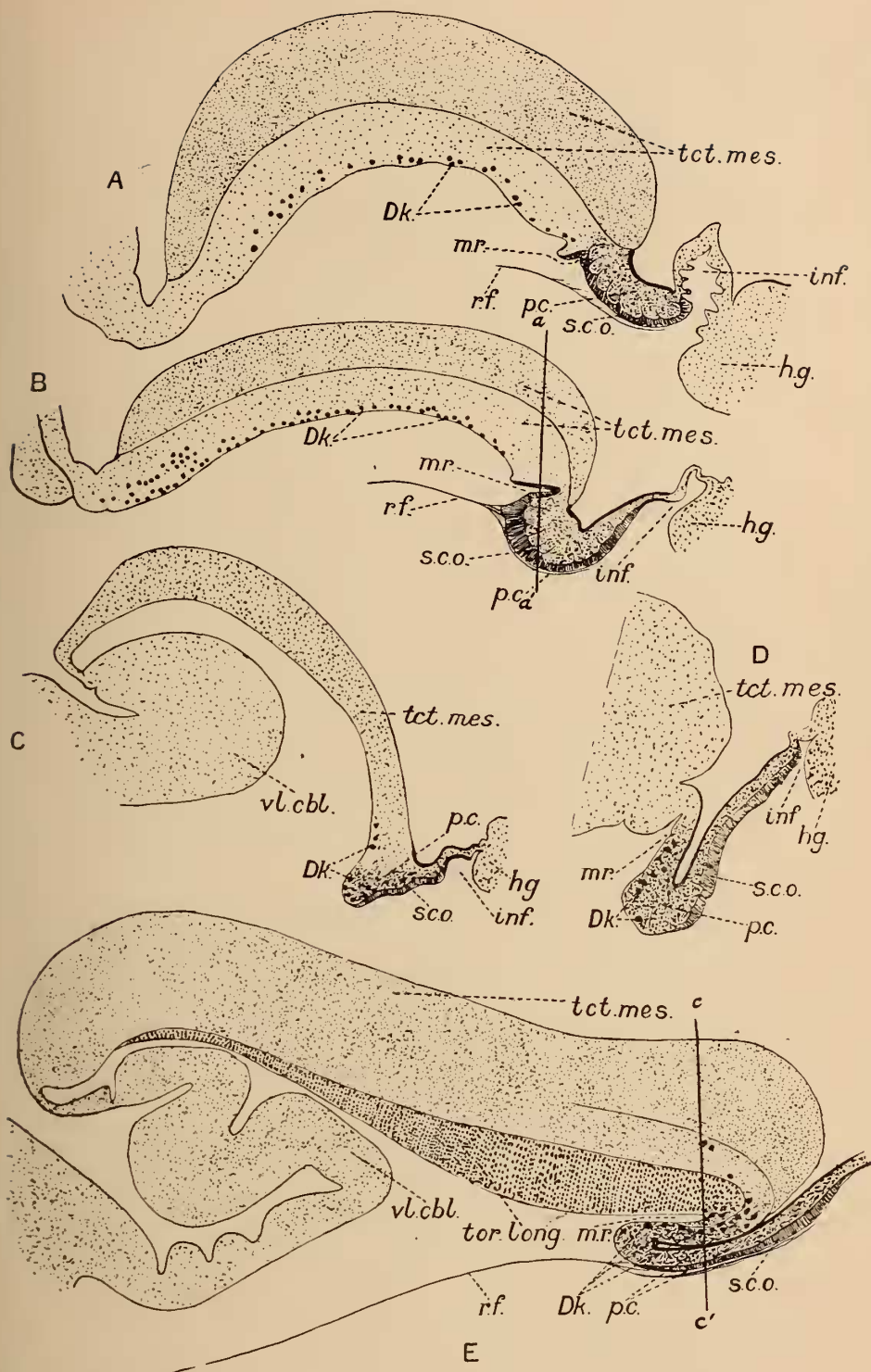
Concerning the "Dachkern" Houser remarks: "It has remained for Sargent (1900) to show that not only is the roof nucleus present in all vertebrates but that it is a part of a most interesting mechanism, the fibre of Reissner" ('01, p. 132). This statement is by no means correct, for although the existence of the cells of this "roof nucleus" had been described in some cases long before in several classes of vertebrates, yet, so far as I can find, this nucleus has never been identified in mammals, nor at that time had it been identified in Teleosts. Subsequently Sargent stated that the *torus longitudinalis* was the homologue of

<sup>1</sup> Studnička ('00), in the previous year, had described and figured this modified ependymal epithelium in *Scyllium*, remarking that he was not able to determine its function, while, so far back as 1892, Edinger ('92) had called attention to it, suggesting that it might have some secretory function.

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TEXT-FIG. 2.—Slightly diagrammatic median sagittal sections through the mid-brains of (A) *Raia blanda*; (B) *Scyllium canicula*; (C) *Polypterus* sp.; (D) *Amia calva*; (E) *Esox lucius*; to show the apparent shifting of the position of the "Dachkern" in fishes. [(D) Has been borrowed from Sargent's ('04) paper, while in (C) the outline has been taken from a figure by Graham Kerr into which the "Dachkern" cells have been drawn from the figure by Sargent ('04, Pl. VI, fig. 41).] *Dk.* "Dachkern." *h.g.* Habenular ganglion. *inf.* Infra-pineal recess. *m.r.* Mesocoelic recess. *p.c.* Posterior commissure. *r.f.* Reissner's fibre. *s.c.o.* Sub-commissural organ. *tect. mes.* Tectum mesencephali. *tor. long.* Torus longitudinalis. *vl. cbm.* Valvula cerebelli. (The lines *ad'* and *cc'* indicate approximately the levels at which the sections represented in Text-fig. 3, A, C, were taken.)

TEXT-FIG. 2.

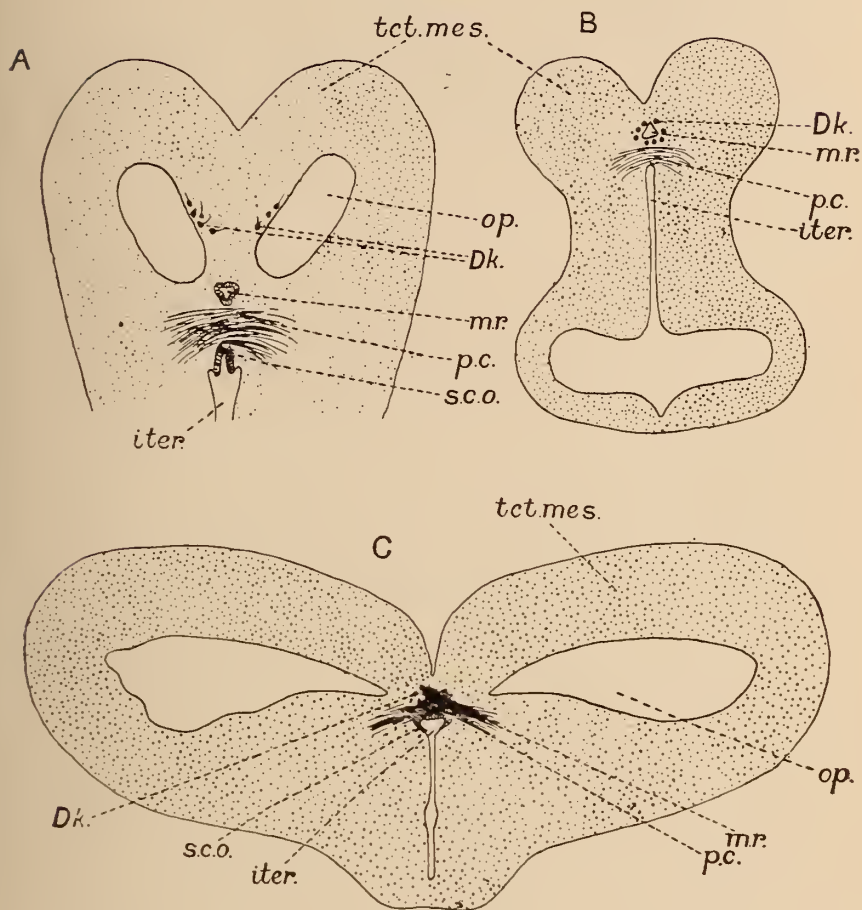


the "Dachkern" of other vertebrates. This suggested homology, as already indicated, I am quite unable to accept, for I shall show that the "Dachkern" is present in a scarcely modified condition in some primitive teleosts in which the torus is also present as a well-developed structure.

That the "Dachkern" has, so far as I can find, never hitherto been recognised in the Teleostean brain is doubtless principally due to the fact that it has apparently shifted its position, and in many Teleosts is greatly reduced in importance, or may even have become obsolete. This apparent change of position is the result of the immense development, in Teleosts, of the tectum mesencephali (the anterior border of which is fixed at the posterior commissure), so that that part of the tectum originally anterior becomes inrolled to form the floor and part of the front wall of the optocœl, where that cavity extends forward above the posterior commissure. It retains, in some Teleosts at any rate, the condition described by Sargent ('04, pp. 188-189, fig. D) for adult Ganoids, and it is remarkable that Sargent, who realised, and, indeed, laid some stress upon the forward shifting of the fore part of the mid-brain, should have overlooked the group of conspicuous cells which occupies in Teleosts a position practically identical with that of the "Dachkern" in Ganoids, and strictly comparable with that occupied by this nucleus in other classes of vertebrates. This question will be more fully discussed when we come to speak of the Teleosts, but in the meantime the above statement may be rendered more intelligible by reference to Text-figs. 2 and 3.

From what has been said it is evident that Houser's observations appear to be quite in agreement with those which Sargent announced in his preliminary papers. In those papers, however, the optic reflex theory had been stated in the barest outline only, and Houser, readily accepting the theory, proceeded to explain and amplify it. In the result, his presentation of the facts and theory

TEXT-FIG. 3.



Slightly diagrammatic transverse sections through the anterior portion of the mid-brain of (A) *Scyllium canicula*; (B) *Acipenser* sp.; (C) *Esox lucius*; to show the relations of the cells of the "Dachkern" to the Tectum mesencephali, Recessus mesocœlicus, and posterior commissure. [(B) is borrowed from Johnston's work on the brain of *Acipenser* ('01). A and C are taken at levels indicated by the lines *aa'* and *cc'* in Text-fig. 2, A and E.] *Dk.* "Dachkern." *iter.* Iter. *m.r.* Mesocœlic recess. *op.* Optocœl. *p.c.* Posterior commissure. *sc.o.* Sub-commissural organ. *tct.mes.* Tectum mesencephali.



prove to be almost entirely different from the account and explanation subsequently offered by Sargent.

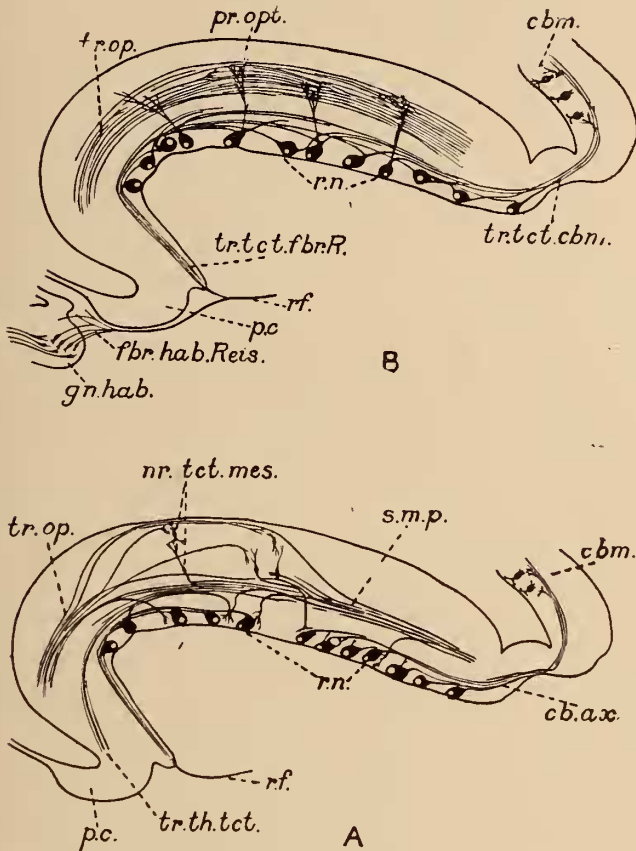
In order that these different accounts may be more readily compared I have, in Text-fig. 4, endeavoured to represent quite diagrammatically what is alleged by these two authors concerning the cellular connections of Reissner's fibre.

As I understand it, Sargent's view (Text-fig. 4, B) supposes that sensory stimuli (optical and olfactory) reach certain cells in the tectum mesencephali (those of the torus in Teleosts, and of the "Dachkern" in other vertebrates), and in the habenular ganglia. These "Dachkern" and torus cells are said to be multipolar, each being stated to give off (i) an "axon," which courses anteriorly to join Reissner's fibre; (ii) a "neurite," ultimately passing posteriorly into the cerebellum, there to "end in fibrillations in the molecular layer" in direct contact with the processes of the Purkinje cells; and (iii) a process which makes its way "towards the ectal region of the tectum opticum," to come "directly in contact with the endings of the proximally running fibres of the optic nerve. It is by this process that the cell is put in direct connection with the outer world by the retina" ('04, p. 168)—the spaced type is mine. The "Dachkern" cells are clearly regarded as motor, for Sargent says that their axons "pass by the shortest route through the ventricle and canal to the posterior portion of the nervous system, where they pass into the cord and probably pass out through the ventral root to the musculature" ('01, p. 450). The habenular cells (which in Cyclostomes, at any rate, are said to be multipolar) also contribute axons to Reissner's fibre, which thus serves "as a short circuit for the transmission of reflexes arising from olfactory as well as optic stimuli" ('04, p. 162).

Sargent also claims that the fibre growing backwards from this cephalic part of the apparatus fuses with "axons" extending forwards from (motor?) cells lying wholly within the sinus terminalis, but nothing is said as to the anterior ending of these latter axons.



TEXT-FIG. 4.



Diagrams representing the cellular connections of Reissner's fibre in the brain, A, according to Houser ('01); B, according to Sargent ('04). *cb. ax.* Cerebellar axons of the "Dachkern" cells. *cbm.* Cerebellum. *fbr. hab. Reis.* Constituent axons of Reissner's fibre derived from cells in the habenular ganglia. *gn. hab.* Ganglion habenulæ. *nr. tect. mes.* Neurons of the Tectum mesencephali. *p.c.* Posterior commissure. *pr. opt.* Processes (dendrites) of the "Dachkern" cells ending amongst the fibres of the Tractus opticus. *r.f.* Reissner's fibre. *r.n.* Cells of the "Dachkern" or roof nucleus. *s.m.p.* Stratum medullare profundum. *tr. op.* Tractus opticus. *tr. th. tct.* Tractus thalamo-tectalis. *tr. tct. cbm.* tractus tectalis cerebellaris. *tr. tct. fbr. R.* Tractus tectalis fibræ Reissneris.

The very delicate strands often to be seen in the *canalis centralis*, that seem to connect the fibre of Reissner with the ependymal epithelium, are evidently the "axons" which are supposed to pass out with the ventral roots of the spinal nerves to the musculature ('04, pp. 188, 195).

According to Houser (Text-fig. 4, A), the *stratum medullare profundum*, which immediately overlies the "Dachkern" is a fibre system into which he claims to have "traced fibres from the cord and oblongata, fibres from the optic nerve, from the neurones of the tectum mesencephali itself. . . . a great tract sweeps into it from the interbrain as a relay in the olfactory apparatus. Fibres are also present from certain of the cranial nerves. All of these fibre systems are to become related to the remarkable mechanism of Reissner's fibre" ('01, p. 125).

Houser thus suggests the transmission along the short cut provided by Reissner's fibre of motor impulses consequent on sensory stimuli other than optic and olfactory, but he indicates paths quite different from those described by Sargent by which the sensory stimuli reach the cells of the "Dachkern." For although he concludes—"It is certainly evident that there are here every means for inter-communication between different parts of the nervous system," yet he traces a connection between this *stratum medullare profundum* and the cells of the "Dachkern," not as Sargent does, but by the passing of some of the fibres from the *stratum medullare profundum* itself down to the "Dachkern" there to end in arborisations over those cells.

It will thus be evident that the two explanations of the working of this optic reflex apparatus have very little in common, and it is, indeed, rather surprising to find Sargent citing Houser as confirming his results.

Moreover, I am quite unable to discover upon what grounds either Sargent or Houser have assumed the motor character of these "Dachkern" cells, for there appears to be absolutely no warrant for the assumption.

It is my own opinion that these large cells forming the "roof

nucleus" will prove to be sensory, and to be simply a part of that series of dorsally placed giant-cells which are such a conspicuous feature in the central nervous system of Cyclostomes and fishes. In support of this view I shall point out that, in *Petromyzon fluviatilis*, the giant cells of the cord do not cease, as stated by Johnston for *P. (Lampetra) wilderi*, behind the commissura infima ('02, p. 5), but extend forwards almost to the cerebellum high up on the medulla on either side of the fourth ventricle. These in many instances project almost through the ependymal epithelium into the ventricle, exactly as the cells of the "Dachkern" commonly project into the mesocoel.

I find, also, a striking similarity in the staining reactions of the cells of the "Dachkern" and of the giant-cells of the cord in those forms where both are developed. Various observers, too, have noticed the failure either of the cells of the "Dachkern" or of the giant-cells of the cord to impregnate with Golgi's method. Further, Sargent remarks that (in young *Raia*) many of the tectal reflex cells are to be seen "apparently undergoing atrophy and degeneration, showing all the stages in the process that have been observed in the atrophy of the dorsal giant-cells of the spinal cord" ('04, p. 166).

In Elasmobranchs, amongst others, the dorsal giant-cells of the spinal cord have been said to completely disappear during embryonic life (Beard, '89, Studnička, '95B), whereas, as I shall describe in a subsequent paper, some, in the hinder part of the spinal cord, are to be found persistent in specimens of *Raia* six to eight inches long, and in adult dogfish. Not only so, but in the latter at any rate they grow to an enormous size and become multinucleate. It is, however, not without significance that some of the cells of the "Dachkern" should be undergoing marked degenerative changes so precisely similar to, and at the same period in development as, many of the giant-cells of the cord.

It is, I believe, now generally accepted that these giant-cells of the cord are sensory, and are derived from neuroblasts

of the neural crests. These neural crests are known to extend forward in development to the front end of the mesencephalon, being interrupted, however, in the region of the ear. The extent of the neural crests, therefore, coincides strictly with the regions in which occur the giant-cells of the spinal cord and the cells of the "Dachkern."

Thus, in their dorsal position adjacent to the cavity of the neural tube, in their general appearance, in their great size, in their possession of one particularly conspicuous non-medullated fibre, in their peculiar staining reactions and in their tendency to atrophy at the end of embryonic life, the cells of the "Dachkern" show a striking resemblance to the giant-cells of the spinal cord.

I have already called attention ('09, '12) to the remarkable elasticity of Reissner's fibre and to its behaviour in recoil in a manner quite unknown among nerve-fibres. Horsley has pointed out that in its failure to show degenerative changes after section it appears quite unlike a nerve-fibre, and this the results of my own experiments, some of which are already recorded ('12), entirely confirm. In its staining reactions, too, the fibre is altogether distinctive.

After continued investigation into the structure and mode of occurrence of Reissner's fibre in all classes of vertebrates, I find myself almost completely at variance with the views expressed by Sargent, and I repeat here the assertion that the fibre is not a nerve-tract. It arises from the specialised epithelium of the sub-commissural organ, which has markedly the character of a sensory epithelium. It is first discernible at a point far forward beneath (anterior to) the posterior commissure, where it is formed by the coalescence of numerous fine fibrillæ, resembling long cilia, from the elongated ependymal cells; these fibrillæ continue to join it along its whole course beneath the posterior commissure (and probably also in the *canalis centralis*); but it never arises, either wholly or in part, from any point in the brain dorsal (posterior) to the posterior commissure in any form which I have studied, except, perhaps, in a comparatively few cases

(e.g. Selachians and Myxinoids), where the specialised ependymal epithelium also may extend onto the dorsal (posterior) surface of the posterior commissure.

### III. REISSNER'S FIBRE AND THE SUB-COMMISSURAL ORGAN IN THE PETROMYZONTIDÆ.

#### *Petromyzon fluviatilis.*

Of this species I have specially prepared and studied seven series of sections of the brain cut in the usual three planes, while of the terminal part of the spinal cord I have five series cut sagittally. In addition to these I have also examined several series through the brain and through the tail region of this animal belonging to the collection of King's College.

Upon the brain of one and another of the several species of this family so much has been written (Ahlborn, '83, on *P. plaueri*; Dendy, '02 and '07, on *Geotria australis*; Johnston, '02, on *Lampetra wilderi*; Sargent, '04 and Sterzi, '07, on *Petromyzon marinus*, to mention only a few of the many modern writers who have dealt with the region of the brain with which I am here principally concerned), that there will be need for me to say very little concerning the gross anatomy of the brain of *Petromyzon fluviatilis*.

#### Sub-commissural Organ.

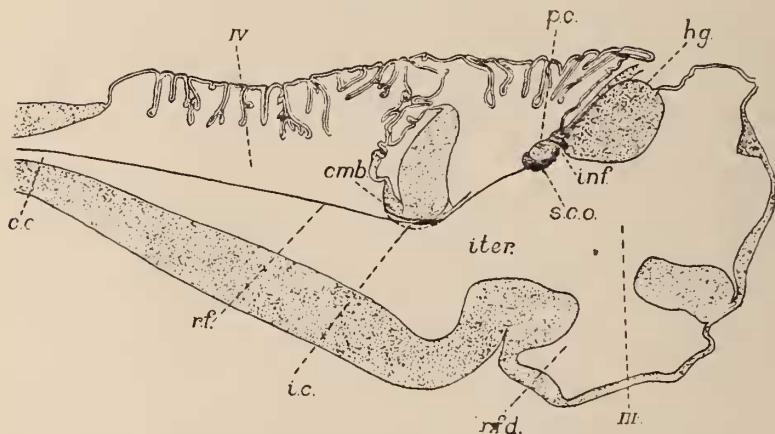
Although a very conspicuous structure, the sub-commissural organ has apparently been described in some detail in three species only, viz.: *Ammocætes* (*Petromyzon*) sp. (Dendy, '02), *Geotria australis* (Dendy, '02, '07), and *Petromyzon marinus* (Sargent, '04).<sup>1</sup> In these, it is

<sup>1</sup> Johnston ('07) does not even mention this structure, and Sterzi merely speaks of a highly developed epithelium lining the "recessi post-abennari" in *P. marinus*. This he supposes (as Edinger before him had done in the case of *Scyllium*) to be a secretory epithelium.

stated to take the form of paired bands of high columnar ependymal epithelial cells, which are grouped so as to bound more or less deep longitudinal grooves, arising anteriorly immediately behind the habenular ganglia and extending backward beneath the posterior commissure.

In *Petromyzon fluviatilis* I find a similar disposition of this characteristic epithelium. It appears anteriorly as a well-defined band in the roof of each of the narrow clefts which separate on either side the downwardly projecting

TEXT-FIG.



A slightly diagrammatic median (sagittal) section through the brain of *Petromyzon fluviatilis*. One of the two factors of Reissner's fibre is shown from the sub-commissural organ backwards, the other branch is indicated near their junction at the anterior end of the isthmus canal. (In a truly sagittal section neither would be seen in front of that point in the mid-brain, for they actually lie just to the right and left of the median plane.) *c.c.* Canalis centralis. *cmb.* Cerebellum. *hg.* Habenular ganglion. *i.c.* Isthmic canal. *inf.* Infra-pineal recess. *inf.* Infundibulum. *iter.* Iter. *p.c.* Posterior commissure. *r.f.* Reissner's fibre. *s.c.o.* Sub-commissural organ. *III.* Third ventricle. *IV.* Fourth ventricle.

habenular ganglia from the side walls of the diencephalon (Fig. 33, *s.c.o.*). Owing to the greater size of the right habenular ganglion the cleft upon that side is almost obliterated and the corresponding ependymal groove crowded out.



It extends forward, therefore, for a much shorter distance than does that of the opposite side, a condition which Dendy ('02, p. 489) noted in the ammocete of *Petromyzon* and, later, in the velasia stage of *Geotria* ('07, p. 5). Sargent states that he found in *Petromyzon marinus* the right groove better developed anteriorly, "corresponding in this with the greater size of the habenula of that side" ('04, p. 152).

Immediately behind the habenular ganglia these lateral clefts (in the roofs of which lie the forward extensions of the sub-commissural organ) widen out into and become merged with the infra-pineal recess. The bands of columnar epithelium also expand, spreading out upon the roof and side walls of that recess (fig. 34). The upper limit of the infra-pineal recess lies at a slightly higher level than the dorsal surface of the posterior commissure, and at that level there are always found a pair of shallow pockets or "diacœlic recesses" bulging very slightly laterally and backward, thus appearing above the posterior commissure. Owing to the spreading out of the paired epithelial bands of the sub-commissural organ upon the roof and side walls of the infra-pineal recess almost all of the upper region of the recess comes to be lined by this epithelium, and the pair of diacœlic recesses are completely lined by it. Being paired laterally placed structures they do not appear in the diagrammatic representation (Text-fig. 5) of a truly sagittal section, but the recess<sup>1</sup> of the right side is shown in fig. 35 (*r.d.*, on the left in the figure), only one being shown on account of the slight obliquity of the plane of the section. From the infra-pineal recess the paired tracts of specialised ependymal epithelium extend downward and backward beneath the posterior commissure, sharply marked off from the general ependymal epithelium. They bound distinct and, for the most part, widely separate grooves,

<sup>1</sup> These recesses appear to be identical with the "recessi postabenu-lari" described by Sterzi ('07) in *P. marinus*. These latter are apparently much larger than the diacœlic recesses I have described in *P. fluviatilis*, and Sterzi seems to have overlooked them in the latter species.

whose lumina face ventro-mesially (figs. 1, 35, 38, *s.c.o.*). This species thus differs from both *Petromyzon marinus* and *Geotria australis*, in which the lumina of the grooves face directly ventrally. It differs, also, from *Geotria* in that, in the latter, the two ependymal bands are in contact mesially.

The epithelium of the sub-commissural organ is composed of elongated, almost fibre-like cells, radially arranged and with deeply seated nuclei which stain very strongly. The cytoplasm of these cells usually stains comparatively lightly, so that, in transverse sections, the sub-commissural organ appears as a pair of pale crescentic areas whose outer bounding curves are defined by closely set nuclei (figs. 38, 39). The inner ends of the cells of the sub-commissural organ are produced into long neuroglia fibres which become collected into bundles and extend to the dorsal surface of the brain, the nerve-fibres of the posterior commissure passing between them.

Laterally the sub-commissural organ is sharply marked off from the general ependymal epithelium, which consists of short columnar cells with more superficially disposed nuclei (fig. 38, *e.ep.*). This general ventricular ependymal epithelium seems to be freely furnished with long cilia, but these are replaced upon the sub-commissural organ by very short, close-set cilia. The latter are not always preserved, but are occasionally quite conspicuous, especially upon that part of the sub-commissural organ which lies in the infra-pineal recess.

Mesially, beneath the posterior commissure, those cells which form the dorsal edges of the grooves are much less elongated, and finally there is a transition into an epithelium of flattened cells which alone cover the ventricular surface of the posterior commissure between the two halves of the sub-commissural organ (fig. 38). This flattened epithelium continues around the hinder end of the posterior commissure and forms the only epithelial covering of the dorsal (posterior) surface of that structure, for onto this surface the sub-commissural organ does not extend in *Petromyzon fluvialis*. Thus, at the hinder end of the posterior commissure

the sub-commissural organ ends abruptly (see Text-fig. 5). Owing, however, to the great length of their component cells the two halves of the sub-commissural organ continue to appear for a short distance in transverse sections as crescentic epithelial structures, lying almost or quite freely in the mesocœl altogether behind the commissure (fig. 36, *s. c. o.*).

This manner of ending of the sub-commissural organ is absolutely characteristic of all the members of the Petromyzontidæ which I have examined. In *P. marinus*, however, Sargent states ('04, p. 152) that the sub-commissural organ ("ependymal grooves") extends around the postero-ventral surface of the posterior commissure onto the dorsal (posterior) surface of that structure, although his figures ('04, pl. i, figs. 6 and 7) do not seem to bear out his statement. I shall return to this matter later.

### Reissner's Fibre.

Springing from the epithelium of the sub-commissural organ, where this lines the infra-pineal recess on either side, a number of delicate fibrillæ may be made out which coalesce to form factors of Reissner's fibre (fig. 39, *fb.*). Mingled with these fibrillæ are numerous fine strands, which I was at first inclined to consider as artifacts due to coagulation. They are, however, invariably present at this point, and closely resemble the constituent fibrillæ of Reissner's fibre, differing principally in that they have a slightly irregular and wavy course, whereas the undoubted constituents of the fibre are straight, as though drawn taut under considerable tension. It may well be that the loose wavy fibrillæ (fig. 39, *fb.*) are simply factors of Reissner's fibre which have been broken and contracted under the action of the fixing reagent.

The sub-commissural organ, as already stated, consists of separate paired bands, which in *Petromyzon fluviatilis* nowhere coalesce nor even closely approach, and it is an interesting fact that in this species the fibrillæ unite to form a pair of principal factors (fig. 37, *r. f.*) of Reissner's fibre.

These remain distinct for a considerable distance through the brain cavity, uniting, in a manner shortly to be described (fig. 11, *r.f.*), to form a single median structure only beneath the posterior part of the tectum mesencephali, immediately in front of the point where that structure joins the cerebellum (Text-fig. 5).

The anterior surface of the posterior commissure, over which the paired ependymal grooves pass, has a presentation approaching the vertical (see Text-fig. 5), but slopes slightly backwards. The course of the paired fibres, therefore, is at first steeply downward and slightly backward. Moreover, they also incline somewhat towards the middle line, and it is thus not possible (in this species) to obtain any considerable length of the fibre in this region in any one (thin) section cut in any of the three conventional planes.

In transverse sections especially the fibre is, in this region, cut very obliquely, and, as it lies in this part of its course closely against the ependymal epithelium, it frequently may, by focussing, be seen apparently penetrating this epithelium. Really, of course, it simply lies against the ependymal epithelium upon its free surface (fig. 38, *r.f.*).

Lying close adjacent to the ventral surface of the posterior commissure, and separated from the aqueductus Sylvii only by that flattened epithelium which extends mesially between the two grooves of the sub-commissural organ, are numerous conspicuous nerve-fibres. These are the axons of the large, laterally situated cells (fig. 36, *n. p. c.*), which Johnston ('02) has identified as the nucleus of the posterior commissure, and they are the nerve-fibres which form, according to Sargent ('04, pp. 154-155, pl. i, figs. 6 and 7), the second of the three sources from which he would derive Reissner's fibre in the lamprey. Owing to the extremely flattened character of the ependymal epithelium here, many of these axons lie quite superficially. Where they pass laterally into the region of the sub-commissural organ they still continue, for a while, to course superficially between the radiating fibre-like ependymal cells, presenting occasion-

ally the appearance of passing out towards the iter. This appearance is to be observed more frequently in transverse sections through the anterior parts of the posterior commissure, where the sections cut its antero-ventral surface very obliquely.

Such a condition is represented in fig. 38, where all the more conspicuous fibres have been carefully drawn in, with the aid of a camera lucida, from an actual section which formed part of a complete series stained with iron-brazilin. As one would naturally expect, these fibres could be followed from section to section, past the point where they might have appeared to emerge, to the side of the posterior commissure remote from that upon which their related cells lay.

It was, perhaps, his failure to interpret correctly appearances such as these that led Sargent to suppose that he could trace axons into the ventricle; while the obliquely cut sections of Reissner's fibre, to which I have already referred as seeming to penetrate the ependymal epithelium, may have been regarded as the continuations of such axons.

The utter improbability of such an origin for the fibre of Reissner, from the confluence of a large number of neuraxons, will become apparent when it is stated that in many instances an individual fibre from this laterally placed group of cells has a diameter as great as, or even greater than, that of the entire Reissner's fibre itself, while collectively (and they are quite numerous) they would vastly exceed that structure in size.

Furthermore, according to Sargent, these constituent fibres form but a fraction of the entire fibre in *Petromyzon*, for other "axons" are described as entering into it (1) from a paired nucleus of large cells, which he correctly homologises with the "Dachkern," and which lies dorsal or dorso-lateral to the posterior commissure, and (2) from large multipolar cells in the habenular ganglia.

As a matter of fact, the ultimate factors of Reissner's fibre are exceedingly fine, and can be traced only to the free surface of the elongated cells of the sub-commissural organ (fig. 39, *fb.*).



Beneath and behind the posterior commissure the right and left halves of the fibre pass backward and ventrally in a nearly parallel course, but converging slightly (fig. 37, *r.f.*), till, beneath the rhombo-mesencephalic fold, they may be seen, in a series of transverse sections, to enter a pair of deep grooves on the ventral surface of that fold (fig. 10, *i.c.*). These paired grooves after a short separate course become confluent behind to form a single median groove, which continues backward to the extreme caudal end of the ventral surface of the fold. This groove, which I propose to call the "isthmie canal" (Text-fig. 5, *i.c.*), is lined by a distinct columnar epithelium, which is much more strongly staining than the ependymal epithelium which covers the rest of the ventricular surface of the rhombo-mesencephalic fold. It is of very general occurrence, at any rate in the lower vertebrates, and probably increases in depth during life. In the Myxinoids, as will be described below, this isthmie canal becomes converted into a tubular structure.

At the point of confluence of the paired anterior parts of the isthmie canal the paired branches of Reissner's fibre also unite to form a single median thread, which lies in the groove close against the ependymal epithelium. In the photomicrograph reproduced as fig. 10, the pair of fibres (*r.f.*) may be seen in the two halves of the isthmie canal at a point about twenty micra in front of the confluence of the canals. In other series of transverse sections through the brain of *Petromyzon*, the isthmie canal does not show the paired anterior portion, and the two halves of the fibre appear to unite slightly antero-ventral to the rhombo-mesencephalic fold (fig. 11, *r.f.*). These are probably younger specimens, for this difference seems to be due to a difference of age and degree of down-growth of the brain-tissue upon the fibre. I have found a similar difference in the frog, where in a young specimen the fibre lies freely beneath the ventral surface of this part of the brain, while in an older (fully grown) specimen the fibre has come to lie in a deep isthmie canal.

Behind the cerebellum the fibre (Text-fig. 5, *r.f.*) emerges



from the isthmic canal and extends perfectly freely through the fourth ventricle, from which it passes into the *canalis centralis* to end in the *sinus terminalis*. In no part of its course does it penetrate the brain-tissue, and the isthmic canal, in all of the seven series examined, remains widely open below. In two series of sections the fibre had evidently broken from its attachment to the sub-commissural organ during the dissection made to expose the brain, and has sprung backward into the central canal of the spinal cord. In both cases, however, the process of fixation must have been well advanced, especially in the relatively less bulky spinal cord, and the fibre has consequently retracted only from the brain into the anterior region of the cord. In one case the recoil has merely resulted in a shortening up of the anterior part of the fibre and a considerable increase in its thickness in that region. In the second case the released anterior end of the fibre has been twisted into a spirally coiled mass of swollen fibre which lies at the point where the fourth ventricle passes into the *canalis centralis*. It is associated with a considerable quantity of dislodged ependymal cells, and on examination it was found that the sub-commissural organ is somewhat incomplete, as though patches of cells had been dragged away when the fibre tore itself free.

Throughout the extent of the *canalis centralis* the fibre is attached, at frequent intervals, to the ependymal epithelium by cilia, which appear to have fused with the fibre, and which probably are, as I have suggested above, actually constituent parts of Reissner's fibre.

I have been able to trace Reissner's fibre with absolute certainty to its actual end in the *sinus terminalis* in this species in but two specimens. This is due to the fact that the fibre can only be certainly followed in sagittal sections, the preparation of which, in this region, presents some difficulty. The spinal cord extends as an exceedingly delicate, tapering *filum terminale* to the extremity of the tail. It is supported ventrally by the notochord, beyond the posterior end of which, however, it projects slightly, there becoming

dilated to partly enclose the sinus terminalis. Above, its meningeal sheath is protected only by the skin, with which it lies intimately in contact. Removal of the skin appears invariably to involve the hinder part of the dural envelope of the spinal cord also, and, as a consequence, the sinus terminalis, of whose wall that envelope forms an integral part. If, however, the skin be not removed, the whole tail becomes greatly crumpled and folded during the processes of paraffin embedding, owing to the considerable shrinking of the skin, which itself becomes at the same time very tough and leathery. Thus, in those series in which the end of the spinal cord had been dissected out (specimens A, B) or in which the skin had simply been removed (specimen C), the sinus terminalis was wanting. On the other hand, in both of the two series of sections (specimens D, E) in which the intact tail region was cut sagittally, it came about that the sinus terminalis, although preserved entire, was unavoidably cut slightly obliquely to the vertical longitudinal plane desired.

A photomicrograph of a section through the sinus terminalis of each of these two latter (D, E) has been reproduced (figs. 12, 13, *s.t.*), while fig. 40 is a composite drawing obtained by superposing camera drawings of four or five consecutive sections of the series through the tail of specimen D.

The sinus (ventriculus) terminalis in *Petromyzon fluviatilis* may be seen in both of my complete series as a somewhat ovoidal space formed by the widening out of the hinder end of the canalis centralis. By Studnička ('95A) it is said to be invariably present in both *P. fluviatilis* and *P. planeri*; Retzius ('95) says simply that in *P. fluviatilis* it frequently occurs.

The anterior part of the wall of this space is formed by the ependymal epithelium of the filum terminale. At about its middle, however, this fails, so that posteriorly the sinus terminalis is bounded only by the confluent connective tissue envelopes of the spinal cord (Fig. 40). The canalis

centralis may thus be said to open freely by a terminal neural pore or foramen into the lymph-space that surrounds the cord. Through this terminal foramen Reissner's fibre passes, to become inserted into, and apparently confluent with, that portion of the meningeal sheath that forms the posterior wall of the sinus terminalis. Its insertion is in the middle line and upon the postero-ventral part of the wall of the sinus.

In fig. 13 the fibre is seen passing across the sinus terminalis to its point of insertion into the wall of that chamber, and in this instance the fibre shows only a slight twisting at short intervals. In the other specimen (figs. 12, 40), the fibre is seen to pass into the apex of a conical mass (*r.f.*) of coiled fibre which lies against the ventro-posterior wall of the sinus and occupies a considerable portion of its cavity.

The descriptions of Studnička ('99) and of Sargent ('04), as well as my own earlier experience (Nicholls, '09), had prepared me for a complete or partial recoil of the fibre in this region. In order to prevent this and to obtain, as far as might be, a representation of the actual condition in the living animal, considerable care was exercised in the preparation of the material. With this end in view, two freshly killed lampreys were taken and immersed whole in the fixing fluid (aceto-bichromate), and, while so immersed, a short stretch of the skin and muscles was removed from one side of the tail to within about an inch from its end to allow of the better and more speedy penetration of the spinal cord by the fixing fluid, without any risk of damage to, or displacement of, the spinal cord and enclosed Reissner's fibre. This last inch or so of the tail was only cut off nearly an hour later, by which time it was supposed that the fibre had become well fixed and its elasticity destroyed. The tissue was then further hardened in the fixing fluid for another twenty-four hours or more.

In the case of specimen E subsequent examination of the sections showed that there had been no post-mortem recoil of the fibre, which could be traced forward uninterruptedly from the sinus terminalis in a perfectly straight line through the canalis centralis. It is thus practically certain that the

slight knotting and coiling to be observed in the fibre (fig. 13) must have existed in life. In specimen D, however, the cord and Reissner's fibre were clearly severed prematurely, before the latter had been quite fixed at its posterior end. A certain amount of recoil had taken place, so that for about three millimetres the canalis immediately behind the point of cutting had had the fibre withdrawn from it. Where the fibre appears it is found to stretch back in a tolerably straight piece almost to the sinus terminalis. About at the point, however, where the central canal begins to widen out, just anterior to the sinus terminalis, the fibre passes into a considerable tangle (fig. 40, *r.f.'*), from the hinder end of which it emerges to run in a short straight course into another and much larger tangled mass (fig. 40, *r.f''*). This second tangle is that conical heap which forms so conspicuous an object in the sinus terminalis (fig. 12, *r.f''*), the base of the cone lying against the postero-ventral wall of the sinus terminalis. Its apex, into which the straight part of the fibre passes, projects dorsally and a little forwards. As a post-mortem recoil has here undoubtedly occurred, it is not now possible to decide whether any of this tangled mass of the fibre was present as such in the living animal. It is my opinion, however, that the intricately tangled mass (fig. 40, *r.f.'*) lying near the end of the central canal is alone sufficient to account entirely for the comparatively small amount of retraction from the anterior end to which I have referred.

In addition to this material which I myself prepared I have examined a number of series of sections through the tail of *Petromyzon fluviatilis* which are in the collection at King's College. In two of these I found the sinus terminalis almost intact, but in one only could Reissner's fibre be traced backwards to that point. In that series, which was cut horizontally, the fibre may be seen emerging from a widely open terminal neural pore as a taut thread, which passes at its extremity into a mass of indeterminate tissue and is lost. The meningeal walls of the sinus terminalis in this specimen are very ill-defined.

In the other series, a sagittal one, the sinus terminalis was cut obliquely. It appeared, however, to be a well-defined globular space. The anterior hemisphere was covered with the spreading flattened ependymal epithelium of the filum terminale, but this was lacking on the hinder half, and here the wall was made up wholly of connective tissue. The sinus itself was filled with a granular coagulum and Reissner's fibre could not be identified.

The effect obtained by a severance of cord and fibre when fixation is still incomplete has already been figured and briefly described by me ('09, '12). The evenly twisted condition of Reissner's fibre, to which I have referred as occurring in those cases where only a gradual recoil of the fibre has taken place, has been observed in the central canal of three different specimens of *Petromyzon fluviatilis*.

The first case of this kind was obtained in the terminal portion of the spinal cord, which had been dissected out from the vertebral canal after partial fixation. The cord and fibre were cut in front and retraction of the fibre has taken place backwardly from that point. In the operation of dissecting out the piece of spinal cord, however, the sinus terminalis was destroyed and the fibre has also retracted forwards, but it appears probable that the retraction took place principally from before backwards, for from the point where the fibre was cut the canalis centralis is empty of fibre for a space of nearly fourteen millimetres. The anterior part of the piece of fibre in question is almost perfectly straight and not greatly swollen. This straight course continues for nearly a millimetre and then the fibre appears thrown into a number of close, tightly wound, corkscrew-like coils which alternate with short straight stretches (fig. 16). Of these corkscrew-like coils some thirty occur in the hinder part of the fibre, which is altogether about three millimetres only in length. The number of turns in any one twisted length varies from four to fourteen, with an average of eight. Occasionally, however, a single turn is found in an otherwise straight piece.

In addition to the coiling there has been an actual shrinking in length and a corresponding increase in thickness, for the fibre, which has normally in the lamprey a diameter of 1.5-2 micra, has here a diameter of 4 micra.

A second instance of such spiral retraction of the fibre was found in the same region of the spinal cord of another specimen. In this the apparently functional fibre is found stretched taut from the sinus terminalis to a point as far forward as my sections go. Close against this fibre, however, there occurs a short stretch of freely lying fibre wound continuously in a fairly open spiral. I find it particularly difficult to account for the presence of this free piece of coiled fibre. It may of course be a remnant of the fibre broken some time previously, but in that case it is remarkable that it should have continued coiled.

The third case is that of the lamprey, above referred to, in which the fibre had broken free from the sub-commissural organ and had retracted into a knotted end in the central canal. For a short distance posterior to the free knotted end the fibre stretches backward as a simple spirally wound thread.

### The "Dachkern."

This remarkable group of large and conspicuous cells has been known under a variety of names, having been termed variously the "mesencephalic trigeminal nucleus" by Osborn ('88), the "nucleus magnocellularis" by Johnston ('01), the "nucleus magnocellularis tecti" by Edinger ('01), and the "mesencephalic nidulus of optic reflex cells" by Sargent ('04). The name "Dachkern" appears to have been first used by Rohon ('77), who applied it to the collection of large cells in the tectum mesencephali of Selachians, and though open, perhaps, to objection, is at least distinctive.

The nucleus has been described by many authors, and in nearly all classes of vertebrates. So far as I can find, however, it has never been identified in mammals, while in Teleosts it has been, as I believe, erroneously (see above) homologised with the *torus longitudinalis* by Sargent ('03 A).



In the Cyclostomes it was first recognised by Sargent ('04) in *Petromyzon marinus*, in which species he has described it (op. cit., p. 154) as consisting of two groups of large cells placed symmetrically on either side of, and at some little distance from, the median plane, each group containing from eight to twelve cells.

Sargent further claimed that he found these large cells in larval specimens of *P. planeri*, but, as I shall presently point out, it is evident that he has, in that ammocœte, altogether failed to interpret correctly the several structures in the roof of the brain, and from his figures it appears probable that the cells which he considers as the mesencephalic nidulus of optic reflex cells do not represent that nucleus at all.

That the cells of this nucleus are, however, present in all the members of the Petromyzontidæ is very probable, although possibly they become very reduced in some species. Thus Johnston was unable to find them in *Petromyzon* (*Lampetra*) *wilderi* ('02, p. 29) while I have not been able to identify them with certainty in ammocœtes of *Ichthyomyzon* (*Entosphenus*) *tridentatus* even in comparatively large specimens (up to 95 mm.). There is, however, in this species, a paired group of large, rather clear nuclei immediately external to the sub-commissural organ, which quite probably represent the "Dachkern."

The nucleus is present in *Geotria australis*, although the cells are not very well defined, in several of the series examined. The want of definition is partly due to the fading of the stain employed, but must be to a certain extent attributed to the fact that these cells appear to stain somewhat capriciously, the cytoplasm taking the stain well, in my experience, only when the tissue as a whole has been rather overstained.<sup>1</sup>

The large cells figured and referred to by Dendy ('07, fig.

<sup>1</sup> That this nucleus has been so long overlooked in the Cyclostomes may perhaps be attributed in some measure to this peculiarity. I believe, also, that they rarely, if ever, take up the silver impregnation of Golgi, which may possibly explain their alleged absence in *P. wilderi*.

3, and p. 17) do not form part of this "roof nucleus," but belong to the nucleus of the posterior commissure. It is in these laterally placed cells that Sargent finds the second source of axons for the fibre of Reissner. The cells of the "Dachkern" in *Geotria* lie comparatively near to the middle line, scattered among the fibres of the posterior commissure immediately dorsal to the sub-commissural organ.

It is principally in *Petromyzon fluviatilis*, however, that I have observed the "Dachkern" in this family. In this species it is moderately well developed, and is found to consist of a somewhat variable number of large cells which lie in the course of the posterior commissure. They are never very remote from the sub-commissural organ, against the inner border of which they mostly lie, either just above or to the outer side. The paired character of the nucleus is somewhat obscured, the cells lying sometimes closely adjacent in the middle line, sometimes trailing out in uneven lines with usually more cells upon one side than the other. Their number, all told, does not appear to exceed two dozen, but it was somewhat difficult to determine accurately their precise number, for, owing to their large size, each may appear in several consecutive sections. Some of the largest cells have a maximum long diameter of about 30 micra with a short diameter of approximately 12 micra. Their size and shape are very variable, but in all there is a large clear nucleus with well-marked chromatin network and one or two nucleoli. The diameter of the nucleus is usually about 10 or 11 micra.

That these cells, in the various *Petromyzontidæ* referred to, represent the "Dachkern" of higher vertebrates admits, I think, of no doubt, but that their axons constitute a part or the whole of Reissner's fibre I emphatically deny. It is, of course, possible that they are related to the cells of the sub-commissural organ, although I have not been able to establish this relation; their principal axons appear to pass with the fibres of the posterior commissure to that side of the brain remote from the cells from which they arise, but beyond that point I have not attempted to trace them.

The second source, according to Sargent, of the constituent fibrillæ of Reissner's fibre is the group of large cells lying somewhat lateral to the two halves of the sub-commissural organ. These, as already stated, are clearly part of the nucleus of the posterior commissure (Cf. Sargent, '04, pl. i, fig. 7, and Johnston, '07, fig. 132).

I have been quite unable to recognise the multipolar cells in the right habenular ganglion from which Sargent supposed a pre-commissural unpaired part of Reissner's fibre to be derived. As already repeatedly stated, I find the fibre arising as a structure, paired even in front of the posterior commissure, from the paired grooves of the sub-commissural organ, the two halves of the fibre remaining distinct in *Petromyzon fluviatilis* practically for the entire length of the mid-brain.

Although perhaps not directly related to the subject of this paper, I propose to make brief mention of certain other large and conspicuous nerve-cells in the roof of the brain. These are situated, in *Petromyzon fluviatilis*, high up on the walls of the hind brain some little way behind the cerebellum. They occur usually just beneath the ependymal epithelium, through which they often appear to bulge so as to lie exposed, practically, in the fourth ventricle. Traced backwards, these are seen to form a paired longitudinal series in which the two lines approach each other till that point is reached where the walls of the hind brain overarch and meet above the fourth ventricle. At this point the two converging lines of large cells become parallel and pass backward as that well-known paired tract of giant-cells which are such a conspicuous feature of the spinal cord of many of the lower vertebrates.

Thus in the common river lamprey these giant-cells do not end, as is said by Johnston ('02, p. 5) to be the case in the brook lamprey (*P. wilderi*), at the commissura infima, but continue forwards in the hind brain to about that point which coincides with the forward limit of the neural crests of the embryo.

In their size and staining reactions these cells in *P. fluviatilis* are practically identical with the large cells which form the "Dachkern" in the lampreys, and which also show evidence of a paired arrangement and have a similar situation on either side of the middle line. Further, the position and extent of the "Dachkern" in all vertebrates in which it is known to occur coincides closely with that of the forward isolated portion of the neural crests of the embryo. In the lampreys it is true that, owing to the roof of the mid-brain remaining largely membranous, the "Dachkern" is restricted to the anterior portion only of that region.

#### *Geotria australis.*

For the opportunity of studying the condition of Reissner's fibre in this species I am indebted to Professor Dendy, not only for the loan of his collection of sections through the brain of the velasia and ammocete stages of this lamprey, but also for placing at my disposal several well-preserved heads.

In all, I have examined eleven series of sections through the brain of the velasia, and one series (cut transversely) of the ammocete brain.

In his paper "On the Parietal Sense-Organs and Associated Structures in the New Zealand Lamprey (*Geotria australis*)," Dendy ('07) has briefly described the condition of Reissner's fibre in the brain, and its relation to the sub-commissural organ ("ependymal grooves"). In an earlier paper ('02) he had described the character of the sub-commissural organ in the ammocete.

These paired "ependymal grooves," which terminate, as such, at the hinder end of the posterior commissure, exactly as they do in *Petromyzon fluviatilis*, nevertheless differ from the grooves in that species in that their shallow lumina are presented almost ventrally (Dendy, '02, fig. 2) rather than mesially as in *P. fluviatilis* (figs. 34, 35, *s.c.o.*). Further, so closely, in *Geotria*, do these grooves approach each other in the middle line beneath the posterior com-

missure that the characteristic epithelium appears in the actual median section of series cut sagittally (Dendy, '07, pl. i, fig. 2). Immediately in front of the posterior commissure there is even an actual confluence for a short distance, the grooves presenting there the appearance of a single horse-shoe-shaped structure which lines the arching roof of the infra-pineal recess. Dendy ('07, pl. i, fig. 3) has figured the condition of the sub-commissural organ, as seen in transverse section, at a point immediately behind the infra-pineal recess. The condition of the sub-commissural organ in the infra-pineal recess foreshadows the condition which has become general along the entire length of the organ in many of the higher vertebrates (figs. 2, 3, 6, 8).

Ahlborn ('83), in his figures of *P. planeri*, has shown indistinctly (figs. 25, 26) what may be the paired ends of the grooves immediately behind the posterior commissure, and an unpaired median ependymal mass well developed beneath the posterior commissure. If this, indeed, represents the sub-commissural organ, we have here a further advance upon the incipient fusion of the grooves in *Geotria australis*. In *Petromyzon marinus*, on the other hand, the grooves appear, judging from Sargent's figures, to be even more widely separated than in *Petromyzon fluviatilis*.

Of the eleven series of sections through the brain of the velasia stage of *Geotria*, seven were cut sagittally and four transversely. In three of these the fibre could not be certainly made out, but the sections in two of these three cases were transverse, and in such sections Reissner's fibre is always particularly difficult to recognise.

In only one of the sagittally cut series of sections did I fail to find the fibre, and in this particular specimen the choroid plexus of the fourth ventricle had been dissected away before the sections were cut, and almost certainly the fibre was carried away at the same time.

In the eight brains in which Reissner's fibre was clearly to be seen it had retained its strictly normal position in only

one instance. It must, however, be remembered that the material had not been preserved for the study of this structure, the animals, in every case, having been decapitated. Under the circumstances, therefore, it is surprising that the fibre had been preserved in the normal position in any. The explanation, in this case, appears to be that, in some preliminary exposure of the brain, blood had found its way into the ventricles, and, clotting there, firmly secured the fibre from recoil. The condition of Reissner's fibre in this specimen is represented in fig. 57. The clot above referred to had filled the fourth ventricle and extended into the mesocœl, but the fibre can nevertheless be readily followed. It may be made out arising from the epithelium of the sub-commissural organ by many fine branches which run together into two principal factors. These unite, midway along the cavity of the midbrain, to form a single thread which passes backwards into the fourth ventricle, traversing a deep isthmie canal upon the ventral surface of the rhombo-mesencephalic fold. Behind the fourth ventricle the fibre may be followed to the end of that part of the *canalis centralis* included in the piece sectioned.

It is important to note that just as the two halves of the sub-commissural organ in *Geotria* are tending to become merged into a single median structure, so also the two halves of the fibre are more completely united. Their union occurs well forward in the mid-brain, whereas in *Petromyzon* and *Ichthyomyzon*,<sup>1</sup> in which the grooves are distinct and widely separated, the two factors of the fibre only lose their identity at a point far more posterior, beneath the rhombo-mesencephalic fold. The isthmie canal in these two latter forms may accordingly show more or less definite traces of a paired character, but in *Geotria* it is a simple median groove.

Three other series of sections also show particularly well the paired origin of the fibre in *Geotria*.

In one of these the whole length of the fibre, from the sub-commissural organ to the end of the piece of the spinal cord

<sup>1</sup> See below.



included, is actually contained in two adjoining sections. It has, however, sprung slightly, so that it lies (in the fourth ventricle) a little out of its proper position, as shown in fig. 20. This retraction has permitted some forward displacement of the point of union of the two halves of the fibre, these apparently meeting beneath the sub-commissural organ (fig. 58). In front of this point the paired fibres spread out into a brush-like end of lesser factors, which have broken free from their attachments and are slightly displaced in the sections. From the cells of the sub-commissural organ many constituent fibrillæ may be seen freely projecting, and these are particularly noticeable in the infra-pineal recess, as Dendy has described and figured ('07, p. 17, and fig. 6).

In another series the anterior end of the fibre closely resembles that just described, having also been slightly displaced anteriorly, so that in neither of these two can Reissner's fibre be actually traced to the cells of the sub-commissural organ. Posteriorly, however, the fibre in this series has recoiled into a tangled snarl which was apparently brought up at the hinder end of the isthmus canal.

In the last of these series the fibre has recoiled forward from the point of section to form a typical tangle beneath the posterior commissure as seen in the photomicrograph (fig. 19). In front of this point the paired factors of the fibre may be well seen.

In the four remaining series in which Reissner's fibre was made out it had in every case retracted into tightly wound knots, in the formation of which the fibre had become torn free from its attachment to the sub-commissural organ. In one case alone the snarl appeared as a mass of coiled and greatly swollen fibre immediately below the recessus infra-pinealis. In two others it occurred in similar form, but at the posterior border of the sub-commissural organ, while in the remaining instance it was less coiled but enormously swollen, and lying freely in the mesocœl. In this latter specimen the diameter of the piece measured varied between  $9.6\ \mu$  and  $18\ \mu$ . The normal diameter of the fibre in *Geotria*

appears to be between  $2\mu$  and  $3\mu$ , although in several instances it was found with a thickness of  $4.5\mu$ , even where there appeared to have been but slight retraction.

### Development.

Of the larval stages of *Petromyzon* I have had no material beyond the single series of transverse sections through the head of an ammocete 57 mm. long, this being the specimen in which the "ciliated grooves" of the sub-commissural organ were described by Dendy ('02).

In this series Reissner's fibre cannot be identified with certainty, nor could the large cells, said by Sargent to give rise to the fibre, be distinguished, although that author stated that he was able to discern these cells in ammocetes of *P. planeri* from 6 mm. to 10 mm. in length.

I have, however, been able to prepare and examine a fairly complete series of sections through the whole or parts of larvæ of *Ichthyomyzon* (*Entosphenus*) *tridentatus*, varying in length from 12 mm. to 105 mm., and while, so far as I could find, the ammocete of this genus does not differ markedly from that of *Petromyzon*, my findings are, nevertheless, markedly unlike those of Sargent, who examined *P. planeri*.

As, so far as I know, the nervous system of the ammocete of this lamprey has never hitherto been described, I propose to give a short account of the condition of the roof of the brain at certain stages in development, dealing simply with those parts of the brain with which this research is chiefly concerned.

### *Ichthyomyzon* (*Entosphenus*) *tridentatus*.

This lamprey inhabits the North Pacific Ocean, and is said to take the place in those waters of the very similar lamprey of the North Atlantic Ocean, *Petromyzon marinus*. Like *P. marinus*, it grows to a large size, and although the adult is not, I believe, easily obtainable, the ammocetes are found

plentifully during the early summer in certain of the rivers which drain the western slopes of the Rocky Mountains, and which seem to form the breeding-grounds of the species.

My specimens, which were collected for me by Mr. W. F. Allen from the Carmel R., California, were preserved entire in aceto-bichromate fluid.

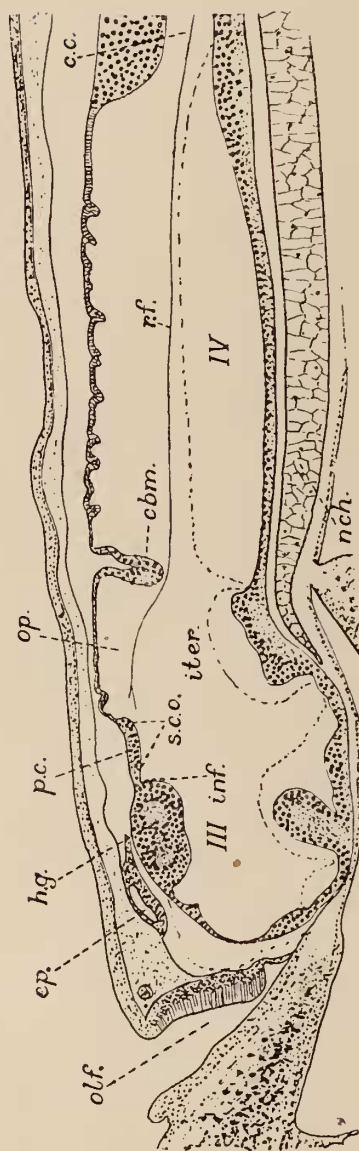
They are of all sizes from 12 mm. to 105 mm. The smallest specimens, I understand from Mr. Allen, were from two to three weeks' old, so that they have apparently a more rapid growth than the ammocetes of *P. planeri*, which were, according to Sargent, from 6 mm. to 10 mm. long at from twenty-six to thirty days after hatching. This difference is probably simply correlated with the considerable disparity in size of the adult animals of the two species and must not be lost sight of, for, as I do not know the ages of my various specimens, I shall be compelled to designate them by their respective lengths, which will probably be much in excess of those of ammocetes of river or lake lampreys of the same age and degree of development.

My smallest specimens included one of 12 mm. and another of 14 mm. which were cut transversely, and others 13 mm. (two) and 14.5 mm. which were cut sagittally.

In all of these the roof of the mid- and hind-brain is still almost entirely epithelial. The plica rhombo-mesencephalica is, however, already well marked, although still only one layer of cells in thickness. At its anterior end the membranous roof of the mid-brain (the future tela choroidea II) passes into the posterior commissure, which, even in my youngest specimens, is quite well defined. Although this has not, as yet, become downfolded to form the plica mesoprosencephalica, its hinder end has already come to lie at a slightly lower level than the developing choroid plexus (see Text-fig. 6).

In the fore-brain the greater part of the roof is occupied by the habenular ganglia, of which the right is enormously the larger. Above these lie the two epiphysial outgrowths, that of the right side being large, and having apparently,

TEXT-FIG. 6.



A median sagittal section through the brain, etc., of a 13 mm. Ammocoete of *Ichthyomyzon* (*Eutosphennus*) *tridentatus*. *cbm.* Cerebellum. *c.c.* Canalis centralis. *ep.* Epiphysis. *hg.* Habenular ganglion. *inf.* Infra-pineal recess. *iter.* Iter. *nch.* Notochord. *olf.* Olfactory opening. *p.c.* Posterior commissure. *r.f.* Reissner's fibre. *s.c.o.* Sub-commissural organ. *III.* Third ventricle. *IV.* Fourth ventricle.

even at this early age, attained its full forward displacement relatively to other structures. All trace of the communication of its lumen with the third ventricle appears to be already obliterated, and as the posterior commissure lies immediately behind the habenular ganglia and at the same level, the recessus infrapinealis (Text-fig. 6, *inf.*) exists as a distinct space principally in that crevice which extends forwards from the posterior commissure for a short distance to the left of the habenular ganglion. Its anterior boundary is already defined by the left Meynert's bundle.

The ventral surface of the posterior commissure is covered by a conspicuous columnar epithelium (figs. 41, 45, *s. c. o.*), plainly disposed in a pair of longitudinal bands which meet in the mid-dorsal line and thus together form a single inverted trough upon the roof of the brain.

The cells of these epithelial bands attain their greatest length laterally, and their nuclei are there deep-seated. Towards the middle line the cells become shorter and have a length scarcely greater than that of their nuclei.

We have thus, at this early stage, a well-developed sub-commissural organ, the two halves of which are not, as yet, sharply marked off mesially from the ordinary ependymal epithelium. The half of the sub-commissural organ on the left side extends forwards into the infra-pineal recess slightly in advance of that upon the right side. Posteriorly the sub-commissural organ stretches, on both sides, the entire length of the posterior commissure, which, at this age, consists of a very thin band, indeed, of transversely coursing nerve-fibres (figs. 41, 45, *p. c.*).

Reissner's fibre may be made out, in sections cut sagittally, arising from the sub-commissural organ by several exceedingly delicate threads, which unite to form a single fibre in the aquæductus Sylvii. Thence it passes backwards as a fine thread freely through the fourth ventricle. It seems to lie against the ventral surface of the plica rhombomesencephalica, but nowhere penetrates the brain tissue, nor is there, at this stage, any trace of an isthmic groove for

its reception on the under surface of that fold (c.f. Text-fig. 6, *r.f.*).

It is exceedingly difficult to recognise the fibre in transverse sections of the brain; in the *canalis centralis* it may, however, be made out, but it is very fine; indeed, its diameter probably nowhere exceeds  $0.3\mu$ , which is its measurement at the hinder end of the fourth ventricle.

The next stage of which I have sections is represented by an embryo of 30 mm. cut sagittally, and a slightly older specimen (40 mm.) cut transversely.

In these, beyond the increase in size of the various parts, there has not been a great deal of change (figs. 42, 46). The choroid plexus of the mid-brain has grown forward so that it now overlies the hinder part of the posterior commissure, and has a well-marked ventrally projecting median fold, much as Dendy has described ('02) for the ammocœte of *Geotria*. (This fold was barely indicated in my smaller specimens.) The posterior commissure still shows no indication of any downfolding, and remains extended horizontally in an antero-posterior direction, on a level with the top of the habenular ganglia.

The sub-commissural organ has increased considerably in size and its two halves are now seen to be somewhat widely separated (fig. 42, *s. c. o.*). At its anterior end the left half of the organ extends forward a short distance in advance of that upon the right side. Posteriorly the specialised ependymal epithelium now extends a little way behind the posterior commissure upon the side walls of the mid-brain in a manner exactly recalling the condition of the ammocœte described and figured by Dendy ('02, p. 490).

Reissner's fibre, too, shows a marked increase in size, having, in the 30 mm. specimen, a diameter of approximately  $0.8\mu$ , measured in the fourth ventricle. The lesser fibres have joined up beneath the posterior commissure into a pair of fibres which remain distinct for some distance, and seem to unite to constitute the single fibre just anterior to the rhombo-mesencephalic fold. In transverse sections the



fibre, though not easily followed continuously through the brain-ventricles, may nevertheless be followed under the cerebellum, and becomes easy to trace in the *canalis centralis* of the spinal cord, where it has a diameter of almost  $1\mu$ .

In an ammocœte 65 mm. in length, the only important feature to note is the development of the isthmic canal upon the ventral surface of the rhombo-mesencephalic fold. This canal in this specimen shows distinct traces of a paired character (fig. 44, *i. c.*).

The right and left halves of the sub-commissural organ have become still more widely separated, and each is now slightly hollowed out to form a groove, the ventro-lateral borders of which are marked off very distinctly from the general ventricular epithelium.

Owing probably to the larger size of this specimen, penetration by the fixing fluid seems to have been less rapid, and the fibre is not quite so well preserved. It has, in the *canalis centralis*, a diameter of barely  $1\mu$ .

Another specimen, 95 mm. long, cut, like the last, transversely, shows some advance upon the condition just described. The sub-commissural organ consists now of a pair of very definite grooves, each somewhat crescentic in transverse section (fig. 43, *s. c. o.*). As in all the other specimens examined, the sub-commissural organ begins in front on the left side, in the cleft between the habenular ganglion and the optic thalamus, and on the right side, somewhat further back, behind the habenular ganglion. The two grooves lie widely apart, have a nearly mesial presentation, and both extend very slightly behind the posterior commissure.

This latter structure has enlarged considerably, and owing to the marked growth of the habenular ganglia, its upper surface now lies at a somewhat lower level than the dorsal surface of those ganglia. Further, from behind, the *tela choroidea* II has continued to grow forward and upward. The posterior commissure, therefore, being left behind by the more rapid growth of the adjacent structures,

seems to be becoming downfolded as the plica meso-prosencephalica. It is, however, still a comparatively thin band of fibres, the upper and lower surfaces of which, as seen in sagittal section, are horizontal.

Upon the ventricular surface of the sub-commissural organ in some sections fairly numerous fibrillæ of Reissner's fibre may be distinguished. The fibre itself passes backwards beneath the rhombo-mesencephalic fold as a single thread, which traverses a deep isthmie canal upon the ventral surface of that fold. In this canal Reissner's fibre lies quite freely. The diameter of the fibre in the fourth ventricle of this specimen is little more than  $1\mu$ .

The study of the posterior end of the fibre is attended with much more difficulty on account of the exceedingly minute lumen of the *canalis centralis* towards its hinder end.

The spinal cord has been stated to arise in Cyclostomes and in Teleosts as a solid cord, its lumen appearing subsequently. In my youngest specimens the lumen has already appeared, and the spinal cord has assumed the appearance characteristic of early vertebrate embryos. In its hinder part the spinal cord is almost cylindrical, and has accordingly, in transverse sections, a nearly circular outline. Owing to the thickness of the walls laterally and to the relative thinness of the median zone the *canalis centralis* appears in such sections as a narrow vertical cleft, which is almost obliterated near the middle of its height. Below it widens into a tiny circular space, and sometimes similarly widens slightly above (fig. 47, *c. c.*).

In the 12 mm. larva this central canal has a maximum transverse diameter of little more than  $4\mu$ , measured at a point about half a millimetre from the end of the body. Forward of that point the lumen is occasionally blocked by an intrusive cell, but behind the canal is entirely free from any such contents.

The *canalis centralis* extends to the hind end of the body, appearing even in the section last but two of this series, which was cut transversely in sections  $10\mu$  in thickness.

In the last few sections the spinal cord narrows into a *filum terminale* (fig. 48), in which the *canalis centralis* gradually widens out into a space, almost square in transverse section, which is enclosed only by a columnar ependymal epithelium, and which must be the *sinus terminalis* (fig. 49, *s. t.*).

This terminal chamber extends through six sections only (60 micra), and has a maximum diameter of  $8\mu$ . It is absolutely free from contained cells of any kind in my youngest specimens.

In many sections through the *canalis centralis* Reissner's fibre can be made out as a very minute dark dot, and may be traced backwards to the *sinus terminalis*, where it is lost.

From what has been stated above of the size and character of the lumen of the central canal at this age, it will be obvious that it is scarcely practicable to trace the fibre in sagittal sections through the tail region, for even where it happened that the plane of the sections was exactly sagittal, the canal was invariably contained within the thickness of a single section. Only in the *sinus terminalis*, therefore, could the lumen be satisfactorily examined, and in this, in both of the 13 mm. specimens and also in the 14.5 mm. specimen, Reissner's fibre may be made out as an extremely delicate thread, which in the longer of these three specimens ends in a swollen knob. This knob appears to be a mass of coagulum (fig. 50, *t. p.*), and in it may be distinguished the remains of nuclei. From the condition, however, in one of the 13 mm. specimens, it would appear that this knob may really represent the terminal plug, which would then apparently have a cellular origin.

In both cases this terminal plug, if it be such, has become detached, and in the smaller specimen it has also apparently been displaced slightly in the preparation of the sections. In both also the *sinus terminalis* opens posteriorly by a small gap in the ependymal epithelium, at a point external to which lies a group of indifferent cells (Fig. 50, *m. t.*) which represent,

probably, the "massa terminale" of Sterzi ('07, p. 303). It seems probable that the terminal plug was, in life, inserted in this gap. Owing to its shape (almost hour-glass in form in transverse sections) the central canal is, at a point just anterior to the *sinus terminalis*, cut twice in sagittal sections, the upper and lower portions of the canal being separated by the bulging masses of the side walls. Reissner's fibre lies always in the lower canal (fig. 48, *c. c.*).<sup>1</sup>

In older ammocetes, however, the central canal has become considerably larger, and the fibre of Reissner may be much more readily traced. As it traverses the central canal it is seen to be joined at short intervals by cilia from the ependymal cells (fig. 56). These attachments seem to be quite strong, for the fibre has deviated slightly from a straight line, and instead of running centrally along the canal has a gentle zig-zag course as though held firmly here and there. The particular instance figured was that observed in the central canal in the tail region of a 34 mm. ammocete, but such a condition of the fibre may be seen in well-preserved material of practically all larval forms, in which, of course, the fibre is still relatively slight. In still older specimens, where the fibre attains a greater size, it appears to follow a more nearly straight course at or near the centre of the canal.

In a larva of 36 mm. the *sinus terminalis* lies immediately dorsal to the extremity of the notochord. It is here an ovoid space almost surrounded by the ependymal epithelium, which is, however, incomplete dorso-posteriorly. Into the gap thus left there is fitted a conical mass, the terminal plug (fig. 53, *t. p.*), from the apex of which, projecting antero-ventrally, Reissner's fibre may be made out running forward.

Another specimen, somewhat older (42 mm. in length), also shows Reissner's fibre ending in a terminal plug (Fig. 51, *t. p.*), which seems to be continuous with the mesenchymatous tissue which lies immediately behind the terminal neural pore.

<sup>1</sup> Cf. the condition of the central canal of *Myxine* and *Bdellostoma* described below.

The terminal plug still retains a postero-dorsal insertion. At this stage the *canalis centralis* is seen to have increased considerably in size, but immediately anterior to the extremity of the *filum terminale* it appears to become more shallow, then deepens and widens into the *sinus terminalis*. Thus, in this particular specimen, the terminal sinus appears conical rather than ovoid in shape. It is probable, however, that the posterior portion of its wall, constituted by the meningeal sheath, has collapsed somewhat, for in a slightly larger specimen (52 mm.) the arrangement of the various structures is precisely similar, excepting that the meningeal portion bulges upwards and outwards, dome-like. It will be noticed that this meningeal portion of the wall of the sinus now lies posteriorly instead of postero-dorsally.

In older larvæ the neural tube has apparently outgrown the supporting notochord and has become turned down behind it. In fig. 52 the posterior end of the spinal cord of a 75 mm. ammocœte is shown partly bent, the bend occurring at the anterior end of the *sinus terminalis*, while in the oldest larva that I have examined (105 mm.), the terminal neural pore has become ventrally directed, and lies below the level of the notochord (figs. 14, 54).

Unfortunately, in none of these older ammocœtes examined (all of which were preserved entire) has the fibre remained in its normal position, but it is broken and ends in a tangle in the *sinus terminalis*.

Such tangles have been found in the terminal sinus of specimens of 65 mm. (fig. 55), 75 mm. (fig. 52), 90 mm. (fig. 15), 95 mm. and 105 mm. (figs. 14, 54). The amount of retracted fibre varies considerably in the different specimens, forming in the cases of the 90 mm. and 95 mm. ammocœtes conspicuous masses of spirally twisted fibre that almost fill the terminal sinus. The condition of the fibre in the 65 mm. specimen is noteworthy, for in this case the recoil seems to have pulled into the terminal sinus some of the fibrous meningeal tissue. The terminal plug cannot be distinguished, being overlain, presumably, by the tangle of Reissner's fibre.

Figure 55 represents the fibre of Reissner emerging from this tangle, and shows also some of the fibrous tissue of the sheath drawn into the terminal sinus. In all of these cases the fibre is enormously swollen.

On the other hand, in the specimens of 75 mm. and 105 mm. the recoils were evidently much less extensive, the break in the fibre doubtless having occurred very far posteriorly. In the latter specimen a quantity of lymphoid matter has intruded through the terminal neural pore, and with this Reissner's fibre (which is not greatly coiled) seems to have become entangled. It may possibly be that we have here a case of incipient regeneration.

In the brain of the ammocœte of *Geotria* the sub-commisural organ is well developed. Its condition has already been described and figured by Dendy ('02, figs. 1, 2), and it differs from that of the ammocœte of *Ichthyomyzon* (*Entosphenus*) *tridentatus* of corresponding age in little but that its two halves are more nearly apposed in the middle line, and that in consequence of this median position the lumina of the grooves are presented almost directly ventrally.

The cilia which clothe the ventricular surface of this organ are short and close set, and amongst them are some longer undoubted fibrillæ of Reissner's fibre. I cannot, however, certainly identify the fibre itself in this region, but beneath the rhombo-mesencephalic fold there is a shallow isthmie canal in which Reissner's fibre may be made out. In the *canalis centralis* of the spinal cord it can be readily traced. Of the tail of this species I have had no material, so that nothing can be stated as to the condition of the fibre and its relation to the *sinus terminalis*.

#### Critical Discussion.

##### (a) The Sub-commissural Organ in the Adult.

It has already been pointed out above that in *Petromyzon marinus*, *Petromyzon fluviatilis*, *Ichthyomyzon* (*Entosphenus*) *tridentatus*, *Geotria australis* and



*Petromyzon planeri* (?) we have apparently a progressively arranged series in the evolution of the sub-commissural organ.

I have further shown that in all the members of this family that I have examined this organ ends abruptly at the hinder border of the posterior commissure, or quickly fades away behind it into the general ependymal epithelium of the iter.

For *Petromyzon marinus*, however, Sargent has given a widely different account ('04), stating that the paired grooves in that species curve around the hinder border of the posterior commissure and pass dorsally (cf. his text-figure A, p. 151) to the anterior extremity of the mesocœl, but, as already remarked, his other figures (Pl. 1, figs. 6 and 7) do not at all bear out his statements. I have not myself examined sections through the brain of this particular lamprey, but assuming that the figures given by Sterzi ('07) represent correctly the extent of the choroid plexus of the mid-brain and its relations to the posterior commissure, it is obvious that the entire dorsal surface of the latter structure lies ventral to this choroid plexus. That being so, the space overlying the posterior commissure, as represented by Sargent in his fig. 7, can only be part of the forward extension of the mesocœl. The two halves of the sub-commissural organ (ependymal grooves) should, therefore, appear in the figure upon the dorsal surface of the posterior commissure if, as Sargent states ('04, p. 152), "Posteriorly both grooves extend . . . downward under the posterior commissure, at the same time coming nearer together. Here they curve around the commissure . . . and continue cephalad into the recessus of the mesocœl above the commissure and thence into its anterior horns. The horns of the recessus are completely lined by this characteristic ependyma. A transverse section through the anterior part of the posterior commissure shows the horns of the recessus as small circular orifices with thick walls composed of this radiating ependyma (pl. i, fig. 6, *rec.* 1')."

The last part of this statement is especially difficult to

reconcile with his fig. 6 (pl. i), for he there shows this recess lying beneath the posterior commissure instead of above it, as described.

Not only are Sargent's statements and figures thus conflicting, but I find nothing in any of the lampreys which I have examined which will throw any light upon the condition which Sargent figures (pl. i, fig. 6)—nothing, that is, of the nature of a postero-dorsal continuation of the sub-commissural organ behind and above the posterior commissure.

I have, however, described paired "diacœlic recesses" (see above) which are shallow pockets bulging caudally from the recessus infrapinealis to overlie slightly the posterior commissure from in front (fig. 35). These recesses are completely lined with the characteristic epithelium of the sub-commissural organ, and in transverse sections through the anterior border of the posterior commissure do present an appearance not unlike that figured by Sargent for the mesocœlic recess. These diacœlic recesses of *Petromyzon fluviatilis* are almost certainly identical with the "recessi postabemplari" of Sterzi, which are apparently particularly well developed in *P. marinus*. An explanation, therefore, which suggests itself in connection with this conflict of statement and figure in Sargent's paper, is that that author may have mistaken the diacœlic recess opening forwardly into the infrapineal recess for a mesocœlic recess opening backwardly beneath the choroid plexus of the mid-brain. An accidental misplacement of a few sections might easily give rise to such a confusion.

#### (b) Development of the Sub-commissural Organ and Reissner's Fibre.

Sargent's account, too, of the development of the fibre is incorrect, which I can only suppose to be due to the fact that he did not recognise the embryonic sub-commissural organ, having failed once again to correctly identify the posterior commissure.

A comparison of Sargent's figures of the brain of the

ammocœte of *Petromyzon planeri* with those of Sterzi ('07, figs. 99 and 124-6) for the same ammocœte, and also of that of *P. fluviatilis*; or with my figures (figs. 45, 46, and Text-fig. 6) of the corresponding structures in *Ichthyomyzon* (*Entosphenus*) *tridentatus* will, I think, convince the reader that what Sargent has named the posterior commissure ('04, pl. i, fig. 2) is undoubtedly the superior (habenular) commissure, while that part of the brain which he labels *tectum opticum* clearly represents the region of the posterior commissure.

Indeed, a comparison of Sargent's own figures (op. cit., pl. i, figs. 2 and 4) bears out this conclusion. In his fig. 4 the epiphysis is seen, cut in transverse section, dorsal to the habenular ganglion, which is perfectly correct for very young larvæ (cf. Sterzi, op. cit., fig. 122). In these young specimens it may also extend backwards to a slight extent, dorsal to the posterior commissure. It continues, however, to grow forward, and, as I have pointed out above, has already, even in my youngest specimens, attained its full forward displacement relative to the other parts of the brain, lying above the anterior region of the dorsal sac.

In his fig. 2, however, Sargent represents it extending dorsally far backwards, behind the posterior commissure, and altogether posterior to the habenular ganglion, a quite unnatural position if the parts were correctly identified. Further, the posterior commissure reaches a size<sup>1</sup> and shape comparable to that of the body so labelled in Sargent's figures only comparatively late in development, by which time the epiphysis has acquired its well-developed eye-like appearance and has an elongated stalk. The right habenular ganglion, on the other hand, has a very precocious development and early reaches a large size, presenting at this age precisely the appearance and relations of the structure which Sargent has named the posterior commissure.

<sup>1</sup> Even in larvæ of *Ichthyomyzon* (*Entosphenus*) *tridentatus* 95 mm. long, the posterior commissure had not such a relatively considerable thickness as compared with its length.

A study of the figures of the development of the brain of any lamprey will confirm these statements.

The existence, too, of a well-developed median brain nucleus in the roof of the brain well behind the posterior commissure (Sargent, '04, pl. i, fig. 3) is altogether incredible, for, as already pointed out, the whole of this region of the brain-wall, at a very early stage indeed, has taken on its permanent character of a cubical epithelium lining the intra-cerebral surface of the tela choroidea. Again, Sargent's description of the position of the "optic reflex cells" behind the posterior commissure in the larva is wholly incompatible with the fact of the position of this nucleus in the adult at a point well forward, dorsal and lateral to the posterior commissure.

All these difficulties disappear when the correction which I have indicated above is made in the labelling of the several parts shown in Sargent's figures, and that author's descriptions, thus amended, would agree very closely with my own observations recorded above.

Sargent is thus, I believe, entirely mistaken in homologising the layer of large cells bulging downwards into the iter with the cells of the "Dachkern" (his "nidulus of optic reflex cells"). The cells of the "Dachkern" in the adult are not so superficial in position and are comparatively few in number (less than two dozen all told), whereas the cells in the group beneath the true posterior commissure in the larva are very numerous (cf. Sargent's figs. 1-3), and even so some of them still appear to be undergoing division. Although, on a casual inspection, the nuclei of these cells seem in the sections to form part of a many-layered structure, a closer examination reveals the fact that this appearance is misleading and is the result merely of the accommodation of the nuclei of a closely crowded group of attenuated cells which are actually arranged to form a single layer investing the under surface of the posterior commissure.

From the ventricular surface of certain of these cells a large cilium (or more probably a group of coalesced cilia)

already projects freely into the ventricle, these being the constituent fibrillæ of Reissner's fibre (Fig. 45, *fb*). For the greater part the cells are still undifferentiated; they are destined, however, to give rise to the cells of the sub-commissural organ, while from their cell bodies grow out the constituent fibrillæ of Reissner's fibre. I am not prepared, of course, to say that no single cell in this group depicted by Sargent in his fig. 3 could form part of the future "Dachkern," but that such cells, if present, send axons into the ventricle, I entirely disbelieve.

(c) Reissner's Fibre in the Brain-ventricles.

In two or three other particulars my observations upon Reissner's fibre in the lamprey are completely at variance with those recorded by Sargent. Thus, in no single instance in any specimen of the *Petromyzontidæ* did I find any part of Reissner's fibre arising from the dorsal surface of the posterior commissure, and I am utterly at a loss to explain Sargent's statements that it arises there. If the sub-commissural organ extends onto that surface there is, of course, no reason why the fibre should not receive factors from that region, but, as I have pointed out above, Sargent's figures do not convey the impression that such a dorso-posterior extension of the sub-commissural organ has any real existence. Sargent's statements, however, imply that not merely does the fibre arise in part from that surface, but that these portions of the fibre constitute its main trunks.

Indeed, the factor from the left side of the brain, according to Sargent, springs wholly from the dorsal aspect of the posterior commissure ('04, pp. 155-6). The part of the fibre which he finds in the diacœle arises, he claims, wholly from the habenular ganglion of the right side, and is collected into a single factor which joins the main right trunk behind the posterior commissure. He could find, he states, no fibre upon the left side traceable to the region of the left habenular ganglion.

Thus, ignoring even the vital differences existing between Sargent's account of the origin of the factors of Reissner's fibre from nerve-cells and my own description of its origin from ependymal cells, I am still unable to reconcile Sargent's description of the course of Reissner's fibre in *Petromyzon marinus* with my own observations upon its path in other lampreys, and, indeed, in vertebrates of other groups.

In the three species of lamprey of which I have examined the brain, Reissner's fibre invariably takes its origin in the infrapineal recess by the union of delicate fibrillæ into a pair of fine threads, which receive constant accessions in their nearly parallel course beneath the posterior commissure. Of constituent fibrillæ from the dorsal surface of the commissure there are none. The paired fibres converge in the mesocœl, and coalesce into a median structure either beneath the rhombo-mesencephalic fold (*P. fluviatilis*) or at some point in front of that (*Ichthyomyzon* and *Geotria*).

Again, in not one of more than thirty lamprey brains (larval and adult) which I have studied have I found the fibre embedded in the brain-tissue of the rhombo-mesencephalic fold as described by Sargent ('04, p. 156). He states: "The fibre passes through this portion of the brain and the basal part of the cerebellum in the median plane a little dorsal to the passage connecting the third and fourth ventricles," and "in both the transverse and sagittal sections that I have studied Reissner's fibre has been found always to enter the right tuberculum acusticum (fig. A)."

In the former statement Sargent has confirmed the description presented by Studnička ('99) of this part of the course of the fibre in *P. planeri*, the latter author having stated that he found Reissner's fibre surrounded by the brain-substance in his two series of sagittally cut sections of the adult brain.

That in the lampreys (as, indeed, in many vertebrates) Reissner's fibre appears in sagittal sections to penetrate the ependymal tissue of the rhombo-mesencephalic fold, I am perfectly willing to admit. That it actually does not do so I am firmly persuaded. Sections cut absolutely truly in the



sagittal plane are not easily prepared, and a very slight obliquity might cause the open isthmic canal to appear as an exceedingly fine tube scarcely larger than the fibre traversing it. Even if the sections were, however, cut perfectly truly, the whole isthmic canal might easily lie within the thickness of a single section, for the full width of the double canal at the point shown in my fig. 10 is less than  $6\mu$ , while behind that point it narrows considerably.

Thus, to determine with certainty whether or no the fibre lies freely, it is necessary to examine sections cut transversely in this region. Even so, it does not follow that the sections so cut will show the fibre, for unless they are prepared with especial care it is more than likely that pieces of fibre may become displaced or lost. It is, therefore, of interest that in the one series which Studnička examined which was cut transversely he found the fibre free ('99 p. 7). This particular series of sections happened to be one through the brain of an ammocœte, and Studnička concluded that the inclusion of the fibre within the substance of the *plica rhombomesencephalica* must take place later in life as a consequence of the downgrowth of the brain in this region.

While, of course, there is nothing inherently improbable in the supposition that the ependymal epithelium of the edges of the isthmic canal should fuse ventrally, beneath the fibre, to form a tube open at either end,<sup>1</sup> I see no reason to suppose that such a condition actually arises in the *Petromyzontidæ*, and I regard Sargent's statements merely as a result of his misinterpretation of the condition observed in sagittal sections.

I have described the occurrence of large snarls in the *recessus infrapinealis* and beneath the posterior commissure (*Geotria*), showing that the fibre, when cut posteriorly, is free to spring forward from its broken end in the central canal of the spinal cord, or equally, breaking free from its attachment to the sub-commissural organ, to spring

<sup>1</sup> Such an inclusion of the fibre within a more or less wide isthmic canal tube actually occurs in the *Myxinoids* (see below).

backward into the fourth ventricle (*Petromyzon*). Nothing of this sort could happen if the fibre were buried in the brain-substance of the rhombo-mesencephalic fold.

(d) The Sinus Terminalis.

As to the universal occurrence of a sinus terminalis there appears to be some diversity of opinion. Both Retzius ('95) and Sterzi ('07) seem to have found this terminal dilatation in some specimens of *Petromyzon marinus* and *P. fluviatilis*; Studnička ('95) found it invariably present in *P. fluviatilis* and *P. planeri*, but he denied that it was present in ammocetes less than 10 cm. long. Schäffer ('01, fide Sterzi) apparently found this terminal dilatation to be constant in all ammocetes. Sargent refers to the sinus terminalis of the ammocete (6-10 mm. in length), but gives no figure, and his figure of the adult terminal sinus is incomplete. I have been able to recognise the sinus terminalis as a dilatation of the terminal portion of the central canal in all of the ammocetes of *Ichthyomyzon* which I have examined, but it is only in specimens of about 40 mm. and upwards that there is an actual bulbous enlargement of the end of the filum terminale. The change of position which this terminal sinus undergoes during larval life is noteworthy. In the young specimens the neural tube stretches wholly dorsal to the notochord and the sinus terminalis lies immediately dorsal to its extremity. The actual terminal neural pore is dorsally directed, and the hinder wall of the sinus terminalis is continuous with the terminal mass of neurenteric cells which caps the end of the notochord. As growth proceeds the sinus terminalis enlarges and begins to turn downward behind the notochord, ultimately coming to occupy the place of the terminal mass. This is not due, however, to an extension of the lumen of the neural tube into the midst of this mass of neurenteric cells as a continuation of the process by which the central canal is said to have arisen. It is to be

attributed rather to the unequal growth of dorsal and ventral surfaces of the filum terminale. The terminal neurenteric mass of cells disappears, and growth appears to go on much more rapidly upon the dorsal surface of the filum terminale. In this way the sinus terminalis becomes carried downward behind the notochord, and as a consequence of this unequal growth the terminal neural pore undergoes a complete change of position. Primarily directed dorsally,<sup>1</sup> it has in turn a postero-dorsal, a posterior and a postero-ventral presentation, and finally takes up an actual ventral presentation.

The sinus terminalis is present in those adult specimens of which I have been able to examine undamaged material, and in every case the terminal neural pore has the ventral position.

#### (e) Reissner's Fibre in the Sinus Terminalis.

In the manner of the ending of the fibre posteriorly, too, the condition in *Petromyzon fluviatilis* and larval *Ichthyomyzon tridentatus* is markedly unlike that which Sargent has described for larval *P. marinus* ('01), adult *P. marinus* and larval *P. planeri* ('04).

According to that author ('04, p. 149) the posterior part of Reissner's fibre arises, in early larval development, by the coalescence of forwardly growing axons from a group of "posterior canal cells" situated wholly within the terminal sinus. This statement was made in the first instance of larval *P. marinus* ('01, p. 448), probably in mistake, for subsequently Sargent states that his investigations of the development of the optic reflex apparatus in Cyclostomes were "confined to the larval stages of *Petromyzon planeri*" ('04, p. 149).

<sup>1</sup> It is of interest to note that in *Amphioxus* (in which I have been unable to determine with certainty the occurrence of Reissner's fibre, although I believe it to be present) there is a sinus terminalis dorsal to the notochord, and with an apparent terminal neural pore, directed, as in young ammocetes, dorsally.

Of adult material, Sargent states that the hinder part of the spinal cord of a single specimen of *P. marinus* was alone examined. From the account which he gives of the preparation of the material, I suspect that the actual sinus terminalis was, partially at least, destroyed, for, as I have already pointed out, the hinder wall of the terminal sinus lies so closely (in *P. fluviatilis*) beneath the skin that the removal of that and the adjoining muscles without injury to the sinus terminalis is a matter of extreme difficulty. In this suspicion I am confirmed by the fact that Sargent offers no description of the terminal chamber, while his figure ('04, pl. i, fig. 3), which professes to represent the terminal sinus, clearly does not do so.

A careful study of Sargent's work shows that, apart from this single tail of *Petromyzon marinus*, he nowhere records the examination of the condition of the sinus terminalis in any other adult vertebrate.

Nevertheless, on the strength of an examination of the condition of this single, almost certainly damaged specimen, he twice ventures ('00, '04) to controvert the account given by Studnička of the mode of ending of Reissner's fibre in *Petromyzon* and *Myxine*. He says ('04, p. 160), "Studnička's statement that the end of Reissner's fibre passes out of the sinus of the ventriculus terminalis and into the surrounding lymph-space is so at variance with all my observations that I must believe the appearance he so interprets was accidental and due to the disturbed and abnormal condition of the fibre in his preparations." (The spaced type is mine.)

As a matter of fact, the account given by Studnička, which was based on the study of a large number of series of sections of several different species, is substantially correct so far as it goes. It is true that the coiled condition of the fibre is probably not normal but due to the recoil of the fibre following some breakage. It is nevertheless a condition very frequently to be observed. Whether, in the case of Studnička's material, this breakage was due to the cutting of the fibre in the fresh

condition in the preparation of the material, or whether the material was hardened entire and the recoil was the result of some breakage of the fibre in life, Studnička in his paper affords no clue. The condition recorded by Sargent was certainly produced artificially by his treatment of his material, and his description of the end of the fibre in adult *Petro-myzon* thus becomes nothing more than an account of a tangle in the hinder part of the central canal, which would apply equally well to a tangle occurring at any point (cf. my figure, '12, fig. 3).

Whether his failure to observe its proper point of ending in the sinus terminalis was due to his failure to trace the *filum terminale* to its end, or, as I think more probable, because the actual extremity of the central canal was lost in the preparation of his material, it is not now possible to determine.

Notwithstanding that his description thus betrays the fact that he himself had failed to discover the normal ending of the fibre in the adult sinus terminalis, he nevertheless disputes the correctness of Studnička's statement that the fibre emerges from the end of the central canal into the lymph chamber which encloses the end of the neural tube.

For this altogether unwarrantable proceeding I can find no excuse. Even if Sargent had correctly observed the condition of the end of the fibre in the ammocete, he was not justified in an assumption that such a condition must necessarily persist in the adult. As a matter of fact, I believe he is also mistaken in his account of the larval condition. I have not examined, it is true, larval material of *P. planeri*, but in a very complete series of ammocetes of *Ichthyomyzon tridentatus*, ranging from 12 mm. to 105 mm. in length, I find nothing to confirm the account given by Sargent of the condition of the posterior end of the fibre in larval Cyclostomes.

The sinus terminalis, as already stated, is present in this species as a terminal dilatation of the central canal, even in my youngest ammocetes. Behind it is blocked by a solid

cellular mass (the terminal mass of Sterzi), which is stated by Goette ('90, fide Favaro) to represent a solid neurenteric connection. Even at this age Reissner's fibre is visible in this region, and ends, apparently, in a conical terminal plug, the origin of which I could not determine. Although my smallest specimens were actually longer than those studied by Sargent, I believe, judging from the condition of the *canalis centralis*, that they were really younger than his specimens.

As I have pointed out above, it is exceedingly difficult to follow the fibre forwards from this point in the smallest specimens on account of the minute size of the central canal. In slightly larger specimens it is, however, possible to trace the fibre as a continuous thread from its origin in the brain to its end in the terminal sinus, but from first to last I could find no indication of the existence of posterior canal cells.<sup>1</sup> In one or two instances intrusive ependymal cells were found in the central canal, but none of these ever happened to occur in the *sinus terminalis*.

#### IV. REISSNER'S FIBRE AND THE SUB-COMMISSURAL ORGAN IN THE MYXINOIDEI.

The heads only of some half dozen *Bdellostoma* (*Polistotrema*) *stouti*, the common hagfish of the Californian coasts, were sent to me by Mr. Wm. F. Allen. Of these I have examined the brains of four in serial section. I have also examined a series of sections through the head of a single specimen of the Cape species of hagfish, *Bdellostoma cirrhatum* (*B. forsteri*). The sections of this last, however, were transverse and quite thick. Further, the stain employed was not the best for the purpose of this investigation. The descriptions, therefore, of the condition in

<sup>1</sup> An examination of a large number of specimens of other larval forms (an account of which will be given in subsequent parts) has given me similar negative results.



*Bdellostoma* will relate to *B. stouti* unless otherwise expressly stated in the text.

Of *Myxine glutinosa* I have had a dozen entire specimens, but of these only two were preserved with any care, being put entire into strong formalin immediately after their capture. The remainder were simply thrown into spirit and had almost certainly been dead for some time before preservation.

It has been remarked by several writers who have dealt with the morphology of the central nervous system of Myxinoids that there is an extraordinary range of variation to be met with in the brains of different individuals. This, my own observations, made upon eight Myxinoid brains, quite confirm.

In particular, this variation is most marked in the extent to which the brain-ventricles have become reduced. In some specimens the cavities of the brain are relatively spacious, while in others they are enormously reduced, and in parts even altogether obsolete.<sup>1</sup>

Those portions of the lumen of the brain which are traversed normally by Reissner's fibre are, however, least variable and are never wholly obliterated, a fact, I believe, not without considerable significance as to the importance of that structure.

My conclusions as to the homologies of the cavities of the mid- and hind-brain agree very nearly with those already put forward by Sterzi ('07). They were, however, arrived at quite independently, and were based principally upon a consideration of the relations of Reissner's fibre and the sub-commissural organ, to which Sterzi, whose work came into my hands only recently, apparently makes no reference. Indeed, it is a surprising fact that of the several workers who have concerned themselves with the histology of the Myxinoid

<sup>1</sup> This may result, I believe, from a continuance late into life of the process of thickening of the walls of the brain, their apposition and fusion, the differences observed then being merely a matter of age.

brain, practically all have failed to refer to the extraordinary development of the ependymal epithelium (of the sub-commissural organ), and to its remarkable distribution upon the ventricular walls.

*Bdellostoma (Polistotrema) stouti.*

In the brain of this animal the reduction of the ventricular spaces has not, in my specimens at least, proceeded so far as is the rule in *Myxine*. Nevertheless, practically the whole of the third ventricle may be obliterated—the infundibular cavity alone persisting—for the so-called “trigonum cinereum,” though frequently present, is apparently not always to be made out. Where the reduction has progressed least there may be found a canal, the “*canalis connectens*” of Holm ('01), which runs upward from the infundibular cavity to join the mesocœlic cavity. Into the “*canalis connectens*” there may open a canal which runs backwards from the trigonum cinereum. In others, this *canalis connectens* may be represented merely by a broken chain of isolated spaces, or even marked only by a band, of varying width, of scattered nuclei, the remains of the cells of the ependymal epithelium which, earlier in life, lined such spaces. Even these traces of a one-time connection may be altogether lost.

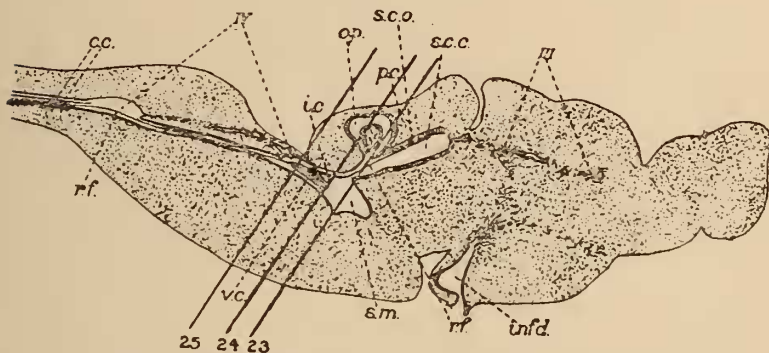
The fourth ventricle, too, is enormously reduced, owing, as I believe, to the fusion of its walls, mesially, at the level of about half the height of the ventricle, followed by the more or less complete obliteration of the upper chamber so cut off from the rest of the ventricle. Here, again, there is considerable variation, the vestiges of the upper portion of the ventricle being much more considerable in some specimens than in others.

The reduction of the ventricles has been least marked in the mid-brain, and the mesocœl forms the most considerable of the brain cavities. Postero-ventrally it is dilated into a large subspherical chamber, which I shall distinguish as

the sinns mesocœlicus (Text-fig. 7, *s. m.*). It continues antero-dorsally as a short wide tube which divides very soon into two canals, one passing anteriorly (figs. 21, 22, and Text-fig. 7, *s. c. c.*), and the other almost directly dorsally (figs. 21, 22, and Text-fig. 7, *op.*).

Of these, that which extends anteriorly is quite constant in its relations. In all my specimens it runs forwards to a point slightly postero-ventral to the habenular ganglia. In one case only was it seen actually to communicate in front with a remnant of the third ventricle. In the others it ended

TEXT-FIG. 7.



A slightly diagrammatic median sagittal section through the brain of *Bdellostoma* (*Polistotrema*) *stouti*. (The lines 23, 24, 25 indicate roughly the levels at which the sections represented in Pl. 3, figs. 23, 24, and 25 are taken. The sections are not, however, nearly so obliquely cut as would appear, for the specimen which was cut transversely was one in which the brain cavities were much more extensive, and in which, therefore, it was possible for the various cavities to appear in sections which were much more nearly transverse.) *c.c.* Canalis centralis. *i.c.* Isthmic canal. *inf.d.* Infundibular cavity. *op.* Optocœl. *p.c.* Posterior commissure. *r.f.* Reissner's fibre. *s.c.c.* Sub-commissural canal. *s.c.o.* Sub-commissural organ. *s.m.* Sinns mesocœlicus. *v.c.* Ventricular canal. *III.* Third ventricle. *IV.* Fourth ventricle.

blindly, the third ventricle being in this region wholly obliterated, and represented merely by the scattered nuclei of its vestigial ependymal epithelium.

In transverse sections (fig. 23, *s. c. c.*, which should be

compared with figs. 21, 22, and Text-fig. 7), this anterior portion of the mid-brain ventricle has a practically circular outline. Its diameter for the greater part of its length remains nearly constant, but increases slightly near the junction, posteriorly, with the second and more dorsally directed canal.

In that portion of the brain which immediately overlies the anterior extension of the mesocœl there is a commissural tract which has been identified by Edinger ('06) and Sterzi ('07) as the posterior commissure, to which conclusion my own observations have also led me. The anterior canal or chamber itself is not, however, I believe, the homologue of the whole of the iter in this region, the greater part of that passage beneath the posterior commissure having been obliterated.

The portion which persists (figs. 21-23 and Text-fig. 7, *s. c. c.*) is completely invested by an extraordinarily developed high columnar epithelium, from which the delicate fibrillæ of Reissner's fibre spring. This epithelium, therefore, represents the sub-commissural organ, and the enclosed space is almost certainly nothing but the product of the complete concurrence of a pair of ependymal grooves. I shall hereafter speak of this canal as the "sub-commissural canal."

I have pointed out above that the two halves of the sub-commissural organ, primarily distinct (e. g. *Petromyzon fluviatilis*), have in *Geotria* united beneath the anterior portion of the posterior commissure to form a median structure, which appears, in transverse section, as a horse-shoe-shaped band.

This tendency towards fusion in the middle line dorsally, seen in *Geotria* alone amongst the *Petromyzontidæ*,<sup>1</sup> has become the rule in higher vertebrates. Not only so, but, since in these higher forms the iter becomes compressed and narrowed from side to side (cf. figs. 4, 7), the ventral edges of the lips of these ependymal bands often nearly meet below (cf. figs. 2, 6). In such cases the iter may be more

<sup>1</sup> *Petromyzon planeri* (?), vide supra.

or less reduced to a tube partly enclosed by the sub-commissural organ. In Myxinoids an actual ventral fusion of the right and left halves of the sub-commissural organ has clearly taken place, and the two grooves have been merged in the single tubular sub-commissural canal. The lower portion of the iter, which existed originally ventral to the sub-commissural organ, has been obliterated. In one of my specimens, however, a trace of this lower portion has persisted as a small canal which runs forwards from the antero-dorsal region of the sinus mesocœlicus. Its course is parallel to, and but slightly ventral to, the sub-commissural canal. At first cylindrical, it gradually tapers away and is lost at a point considerably posterior to the anterior end of the sub-commissural canal. It is lined by ordinary columnar epithelium, and at its posterior end is separated from the sub-commissural organ by but a slight thickness of nervous tissue.

It was in this same specimen, too, that the third ventricle was least reduced, a small canal lined by flattened epithelium continuing forward the lumen of the sub-commissural canal for some distance into the 'tween brain. A small isolated chamber lying dorsal and anterior to the sub-commissural canal apparently represents a reduced infra-pineal or a diacœlic recess.

The second division (figs. 21-23, Text-fig. 7, *op.*) of the short wide canal leading from the sinus mesocœlicus, which I have spoken of as more dorsally directed than the sub-commissural canal, is apparently much more variable. The epithelium, too, which lines it, is, over the greater part of its extent, much less developed, and is markedly elongated only in the region immediately adjacent to its junction with the sub-commissural canal. There can be little doubt that this dorsal or postero-dorsal canal in the upper portion of the mid-brain represents the cavity of the optic lobes of the higher vertebrates, and is equivalent, therefore, to that large space which, in the Petromyzontidæ, lies above and behind the posterior commissure. In the Myxinoidei, however, the

roof in fore-, mid- and hind-brain brain has developed a nervous layer over its whole extent which may become exceedingly thick. At the same time the thickening of the walls of the brain has proceeded to such an extent that, as already stated, the third ventricle has been almost wholly, and the iter largely, obliterated.

In the region of the optic lobes it appears probable that the thickening must have first reduced the optocœl to a flattened circular or discoidal space. The apposition of the opposite walls over a considerable area in the middle of this space must have followed. In the result the optocœl has become a more or less annular cavity. Several stages in the reduction of the optocœl may be observed in the brains of my specimens of *Bdellostoma*.

In the specimen, already referred to, in which the ventricles have been least reduced, the optocœl is seen to have retained this almost perfectly annular shape. This same condition was observed in a second series, which was cut slightly obliquely to the sagittal plane, and is represented slightly diagrammatically in Text-fig. 7, which was obtained by the superposition of camera drawings of several adjacent sections.

In a third specimen (fig. 21) the posteriorly recurved portion of the optocœl no longer opens ventrally into the iter, and a further stage of reduction of this cavity is shown in the fourth specimen (fig. 22), where the hinder part of the optocœl has been altogether suppressed. The latter photomicrograph shows particularly well the highly developed epithelium (*s. c. o.*), which lines the sub-commissural canal (*s. c. c.*) and is continued into the optocœl upon its anterior wall, where it clothes the posterior surface of the posterior commissure.

In every case, however, there is a rapid transition from the extremely elongated cells of this epithelium into a much shorter columnar ependymal epithelium in those parts of the lumen remote from the posterior commissure.

The short common canal formed by the junction of the sub-commissural and optocœlic canals leads postero-ventrally into



the sinus mesocœlicus (Text-fig. 7, *s. m.*; figs. 21, 22, *s. m.*', *s. m.*''). This chamber, which, as already stated, forms by far the most considerable of the brain ventricles, must be regarded as equivalent to the hinder portion only of the iter of other vertebrates.

Sanders has described this chamber (in *Myxine*), as seen in sagittal section, as like a pipe-bowl in shape, and this description would apply equally well to the sinus mesocœlicus of *Bdellostoma*. In this latter animal, however, it is partly separated by a marked horizontal constriction into upper and lower chambers (figs. 21-23, *s. m.*', *s. m.*''). It is into the upper chamber that there opens the small anterior prolongation of the iter above referred to.

The horizontal constriction becomes more pronounced posteriorly, and finally forms a distinct horizontal partition which completely separates the two chambers (fig. 24). The two chambers so formed are at first of nearly equal size and are separated only by an epithelial partition. Further back the dividing lamella becomes much thicker and the two spaces become reduced in size and canal-like.

The upper one (fig. 24 and Text-fig. 7, *i. c.*), the posterior continuation of the upper chamber of the sinus mesocœlicus, is, without question, the homologue of the isthmus canal of the *Petromyzontidæ*, and must be considered as part of the mesocœl. It passes backwards with but slight alteration in size, but loses its circular outline (fig. 25, *i. c.*) and becomes flattened dorso-ventrally. Presently it opens widely, ventrally, into the fourth ventricle.

The lower canal (fig. 24 and Text-fig. 7, *v. c.*), which I have called the "ventricular canal," diminishes in size very rapidly, and, after separating somewhat widely from the isthmus canal, again approaches it (fig. 25), the two ultimately reuniting to constitute the fourth ventricle.

At the point of junction of these canals there is a slight dilatation (Text-fig. 7), but through the greater part of the extent of the medulla oblongata the fourth ventricle is chiefly represented by the narrow posterior continuation of

the ventricular canal. It is lined by a very ordinary short columnar epithelium.

In the thickened roof of the fourth ventricle there is, however, a chain of small, discontinuous and somewhat irregular spaces lined by a flattened epithelium, which continue backwards in the middle line directly dorsal to the fourth ventricle (Text-fig. 7). The most anterior of these spaces is, in one specimen, barely separated from the anterior dilated portion of the fourth ventricle by an epithelial wall.

Frequently these small spaces are divided vertically by a nearly median partition, and then appear as paired cavities lying on either side of the middle line. In one case there was a median space with a small lateral chamber on either side. It is clear that collectively they represent the vanishing vestiges of the dorsal portion of the fourth ventricle. I was able to make them out most satisfactorily in a series of sections cut transversely. In other series, cut sagittally, they are much less conspicuous.

In every brain examined, however, there was to be observed towards the hinder end of the medulla oblongata, at the level of these vestigial ventricular spaces (and therefore well above the continuous tubular portion of the fourth ventricle), a considerable space. This, which is to be regarded merely as an enlarged member of the dorsal chain of small spaces, is in wide communication below with the fourth ventricle in one specimen only (Text-fig. 7). In the three remaining specimens it is separated from the fourth ventricle by a thin layer of epithelium. Just behind the communication between the two cavities (where such communication occurs) the upper space tapers off into a narrow canal, which runs backwards dorsal and parallel to a similar backward continuation of the ventricular canal, the two giving rise to the double canal so characteristic of the spinal cord of the Myxinoidea. I look upon the dilatation of the last member of the upper discontinuous series of spaces as indicating approximately the hinder end of the medulla oblongata.

Reissner's fibre arises at the forward extremity of the mid-brain in a very large number of exceedingly fine fibrillæ from the cells of the sub-commissural organ surrounding the sub-commissural canal. These join together to form fine threads, which, in one specimen, are definitely seen as a pair of larger factors. These are situated nearly centrally in the sub-commissural canal, and become stouter as they pass backwards from their brush-like origin. At a point near the middle of the length of the sub-commissural canal the lesser fibres join up into the very definite fibre of Reissner, the diameter of which is seen to increase markedly as it is followed backwards.

In the one series cut transversely the fibre could not be followed. In another series (cut sagittally) it has sprung forwards from the *canalis centralis*, to lie, as a thickened rod, in the dorso-posterior portion of the *sinus mesocœlicus*. In both of the remaining specimens it has preserved its normal position, and may be observed as a tautly stretched thread (fig. 22, *r.f.*) passing from the sub-commissural canal through the upper chamber of the *sinus mesocœlicus* and so into the isthmic canal. From this it emerges into the fourth ventricle and passes backwards along the lower of the two divisions of the *canalis centralis* of the spinal cord (figs. 31, 32, *r.f.*). In the section photographed for fig. 21 a considerable length of Reissner's fibre occurs in the isthmic canal, but the magnification is too small to render the fibre visible.

The sub-commissural organ, owing to the complete fusion of its two halves ventrally as well as dorsally, has assumed the shape of a test-tube with its sealed end forward (the sub-commissural canal, figs. 21-23, and Text-fig. 7, *s.c.c.*). It slopes backwards and downwards beneath the posterior commissure, which is very ill defined and which appears to extend through nearly half of the length of the mid-brain. Behind the posterior commissure the upper half of the sub-commissural organ bends dorsally into the *optocœl*, where it passes gradually into a more ordinary columnar epithelium.

Ventrally it ends abruptly, being quite sharply marked off from the epithelium of the sinus mesocœlicus.

The actual cells of the sub-commissural organ are, like those of the Petromyzontidæ, extremely elongated and fibre-like. In both *Bdellostoma* and *Myxine* they attain a length of about  $50\ \mu$ , or approximately half of the diameter of the sub-commissural canal.

The fibrillæ of Reissner's fibre spring most freely from the anterior portion of the organ, but some continue to join the fibre along the whole extent of the sub-commissural canal. I have not been able to detect any fibrillæ arising from the epithelium which passes into the optocœl, though it is not improbable that some strands may actually have their origin there. In one specimen, indeed, a very fine factor appeared to issue from the optocœl to join Reissner's fibre.

#### *Bdellostoma cirrhatum.*

In the single series of sections through the brain of this species Reissner's fibre can only be seen in some sections. The sections were transverse and very thick, and the fibre had doubtless fallen away (it being in thick transverse sections difficult to attach the sections of fibre sufficiently to the slide). The ventricles of the brain very closely resemble the condition described as occurring in that specimen of *B. stouti* in which they had been least reduced. The cavity in the upper part of the hind-brain is relatively spacious and in open communication with the fourth ventricle. In the mid-brain there is a quantity of coagulum which, both in the sinus mesocœlicus and in the ventricular canal, might be mistaken for tangled and netted masses of Reissner's fibre. It was probably some such condition as this which misled Ayers (see *infra*).

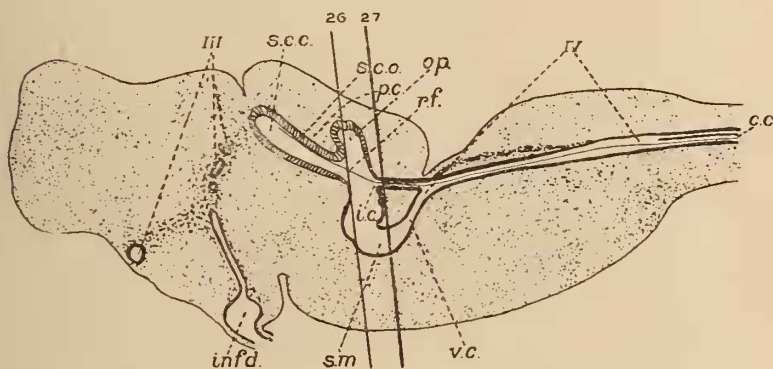
#### *Myxine glutinosa.*

Of this species all but two of my specimens had been preserved entire in alcohol. As spirit usually penetrates

much more rapidly than does formalin I was rather surprised to find that while the formalin-preserved material gave me quite good results the spirit material was much less satisfactory. I can only suppose that this latter had been dead for some time before preservation was attempted.

Text-fig. 8, which, like the corresponding figure of *Bdellostoma*, was obtained by superposing camera drawings of several adjacent sections, represents diagrammatically the condition of the brain of *Myxine* as seen in sagittal section, and the course of Reissner's fibre through the ventricles.

TEXT-FIG. 8.



A diagrammatic median sagittal section through the brain of *Myxine glutinosa*. (The lines 26, 27 indicate approximately the planes of the transverse sections reproduced in Figs. 26 and 27.) c.c. Canalis centralis. i.c. Isthmic canal. inf.d. Infundibular cavity. op. Optocœl. p.c. Posterior commissure. r.f. Reissner's fibre. s.c.c. Sub-commissural canal. s.c.o. Sub-commissural organ. s.m. Sinus mesocœlicus. v.c. Ventricular canal. III. Third ventricle. IV. Fourth ventricle.

Like that of *Bdellostoma*, the brain of *Myxine* is exceedingly variable, but in none of the three brains examined has there remained any trace of an open connection between the ventricles of the fore- and mid-brain.

In the mesocœl in every case five distinct chambers could be recognised. A well-marked sub-commissural canal (s. c. c.), completely invested by the highly specialised epi-

thelium of the sub-commissural organ (*s. c. o.*), and an optocœl (*op.*), which appears as a short bluntly ending and dorsally directed canal much more reduced than the corresponding canal in *Bdellostoma*, both open postero-ventrally into the sinus mesocœlicus (*s. m.*). From this, two canals, isthmie (*i. c.*) and ventricular (*v. c.*), lead backwards, but whereas in *Bdellostoma* it is the isthmie canal which is much the larger, in *Myxine* the ventricular canal is large and the isthmie canal has become a very narrow channel (compare figs. 25 and 27).

The latter opens widely into the upper portion of the sinus mesocœlicus on the level of the posterior end of the sub-commissural canal, but diminishes rapidly (funnel-wise) and extends through the greater part of the thickness of the postero-ventral portion of the optic lobes as a very fine canal, nearly oval in transverse section and comparatively remote from the backwardly-bulging sinus mesocœlicus.

The sinus mesocœlicus at its lower end is somewhat constricted and passes into the ventricular canal, which curves upwards and backwards to meet the isthmie canal as it makes its exit from the mid-brain. The junction of the two canals marks the beginning of the fourth ventricle, which, as in *Bdellostoma*, comes, at this point, more nearly to the dorsal surface of the brain than elsewhere. In *Myxine*, indeed, it is separated from the vascular tissue which everywhere envelops the brain by a thin layer of epithelial tissue only.

Posteriorly the roof of the hind brain thickens considerably, and again as in *Bdellostoma*, a series of small irregular chambers are to be made out beginning from a point immediately behind the posterior end of the isthmie canal. In some specimens they actually begin on either side of the isthmie canal, at its point of junction with the ventricular canal, as a pair of small chambers. Thence they extend in the middle line backwards to a point near the middle of the length of the medulla oblongata. Beneath this series of small chambers the fourth ventricle passes backwards, changing



in shape, as seen in transverse sections, through triangular to oval and oblong. Finally, it becomes circular, narrowing continually until it has a diameter scarcely greater than that of the *canalis centralis*, into which it presently passes.

At that point, however, where the upper discontinuous remnants of the fourth ventricle cease, I found in two of my specimens a considerable space (fig. 30, *x.*), which appears to be without epithelial lining. It is, nevertheless, lined, I believe, by an extremely flattened epithelium, the sparse nuclei of which are dotted at irregular intervals upon its surface. In one of the two specimens in which the cavity is present, greatly attenuated epithelial cells separate the chamber from the underlying fourth ventricle. In the other example the two cavities are in open communication.

At the posterior end of the medulla the fourth ventricle passes into a double *canalis centralis* (text-fig. 8, *c. c.*), but whereas in *Bdellostoma* (fig. 31) the upper canal is considerably the larger, in *Myxine* (fig. 28) the two canals are of much the same size.

Reissner's fibre (text-fig. 8, *r. f.*) has a course practically identical with that of the fibre in *Bdellostoma*. It arises in precisely the same way from a brush-like mass of delicate fibrillæ near the anterior end of the sub-commissural organ. These, however, appear to unite into a single thread which lies closely against the epithelium of the sub-commissural organ (fig. 26, *r. f.*). It traverses the upper part of the sinus mesocœlicus, and passes into the isthmic canal, lying closely against the upper wall of that passage (fig. 27, *r. f.*). Emerging from the isthmic canal it extends backwards through the fourth ventricle (fig. 30, *r. f.*), and where that gives place to the double canal of the spinal cord it passes into the lower of the two canals (figs. 28, 29, *r. f.*), exactly as in *Bdellostoma*.

It apparently extends through this lower canal practically to the extreme posterior end of the body. Slightly in front of the actual extremity, however, the two canals reunite to form a single canal which appears in transverse section as a

rather narrow vertical cleft. The spinal cord itself turns downwards behind the end of the notochord and becomes enlarged to partly enclose the large sinus terminalis. I was able to make out this condition in but one of the three tails examined in sagittal section; the other two had become twisted during the preparation of the material for sectioning, and in consequence were cut so obliquely as to be unintelligible.

Both Sanders and Studnička seem also to have found such a terminal sinus, and there appears to be no reason to doubt that this is the normal condition of the end of the spinal cord.

In the one specimen examined, the walls of the sinus are clothed antero-dorsally by the ependymal epithelium of the *canalis centralis*, but posteriorly the space is enclosed only by the connective tissues of the meninges. We have thus in *Myxine* a sinus terminalis into which the *canalis centralis* opens by a terminal neural pore exactly as in the *Petromyzontidæ*.

Through this terminal neural pore Reissner's fibre passes, and, in the one specimen in which the relations of these parts could be clearly made out, ends in a large intricately coiled mass, which Sanders has aptly described as a "a mulberry-like mass of glass-like aspect."

A central section through the mass is shown in fig. 18, which is reproduced from an actual photomicrograph. The sections had been stained simply with borax-carmin in bulk, and the mass of fibre was only faintly tinged with pink. After the photomicrograph had been taken the sections were double-stained with picro-indigo-carmin. The coiled terminal mass of fibre became stained green or blue-green in a manner absolutely unlike that in which a nerve-fibre stains. Another photomicrograph was taken, this time of a section nearer to the surface of the mass, and is reproduced as fig. 17. This shows some loose coils of Reissner's fibre lying near the apex of the mass, and close to the opening of the terminal neural pore.

The photomicrographs are not nearly as perfect as I could

wish, and do not represent at all adequately this wonderful mass of fibre; it was, however, a particularly difficult subject to photograph, both on account of the staining and also on account of the thickness of the sections ( $20\ \mu$ ).

Some idea of the relatively enormous size of this mass of coiled fibre may be formed when it is stated that it appears in four or five adjacent sagittal sections, each  $20\ \mu$  in thickness. It thus probably had a thickness of not less than  $80\ \mu$  from side to side. Measured dorsi-ventrally the mass has a length of close upon  $100\ \mu$ , while its average antero-posterior diameter is nearly  $80\ \mu$ .

The *canalis centralis* a little forward of the *sinus terminalis* is empty of fibre, and I estimate that the mulberry-like mass represents some 200 to 250 mm. of fibre retracted into a heap barely 0.1 mm. high. Since the specimen was little over a foot in length I can only suppose that the fibre must have snapped at a point very far forward. This breakage must have been followed by a continuous recoil of the hinder piece into the *sinus terminalis*, such recoil having been completed before fixation was effected.

Sagittal sections through the tail of a second specimen appeared to show a somewhat similar condition, but the sections were so crumpled and distorted in this region that it is not possible to speak with certainty.

Such a condition is, however, undoubtedly of frequent occurrence (Sanders '94, Stodnicka, '99), and must be the result of a breakage of the fibre at some time shortly before fixation. It is certainly not the condition of the functional fibre, which should be inserted, as in the *Petromyzontidæ*, as a tautly stretched thread, into the meningeal portion of the wall of the *sinus terminalis*. This normal condition has, so far as I can discover, been observed only by Sanders ('94, p. 11).

#### Critical Discussion.

As already noted, an account of the occurrence and relations of Reissner's fibre in *Myxine* was given by Sanders as

long ago as 1894. That author was the first to trace the fibre forwards into the mid-brain and backwards into the sinus terminalis, and he, too, was the first to point out that the canal centralis was widely open posteriorly (in *Myxine*), and that through this opening Reissner's fibre passed. Apparently he had formed no definite opinion as to the character of this "central rod," as he called it, in *Myxine*, although in an earlier paper he had accepted Stieda's dictum that it was merely an artifact.

His account of the splitting of Reissner's fibre in the fourth ventricle into two portions, one of which passes through the isthmic canal and the other through the lower canal (the ventricular canal of my descriptions), is, however, erroneous. It is true that in material that is not well preserved there is found a quantity of coagulum which presents the appearance of a network of fibres, and which might be mistaken for Reissner's fibre. In well-preserved material, however, this is absent, and the unmistakable fibre stretches tautly from its point of origin in the anterior part of the sub-commissural canal through the upper portion of the sinus mesocœlicus, and thence through the isthmic canal, nowhere receiving any conspicuous factor or giving off any important branch. The ventral portion of the sinus mesocœlicus and the ventricular canal are not in any of my specimens traversed by the fibre of Reissner. Indeed, I have suggested that the portion of the mesocœl which I have termed the isthmic canal has persisted in *Myxine* (when other portions of the brain-ventricles have been obliterated) because it is traversed by Reissner's fibre.

Studnička, whose findings, in other respects, confirm those of Sanders, says nothing of any part of the fibre passing elsewhere than through the isthmic canal.

The only other observations upon Reissner's fibre in *Myxinoids* are, I believe, those recorded by Ayers ('08). Although he does not refer to it by that name, but speaks merely of "ventricular fibres," I think that there can be no doubt that it is to Reissner's fibre that his work relates. He

speaks of the optocœl as the "cerebellar ventricle," and clearly regards the isthmie canal as part of the fourth ventricle, and claims to have found numerous branches of the fibre issuing from the "mid-brain ventricle" (the sub-commissural canal of my descriptions) and the "cerebellar ventricle" to join a main fibre. This main fibre was found only as a much coiled thread in the "fourth ventricle" (the sinus mesocœlicus and isthmie canal of my descriptions).

He speaks, moreover, of having examined the fibre "in section and by dissection" (my spaced type), which is rather a remarkable statement, for in none of my specimens does the fibre exceed  $2\mu$  in diameter, and it is visible only under quite considerable magnification. It is clear, however, from his description, that the fibre must have been broken or cut prior to the preservation of his material, and that a considerable length had retracted into the sinus mesocœlicus. Some loose loops, perhaps, may have been thrown into the optocœl and so account for the condition he describes. As already stated I found only in a single specimen (*B. stouti*) a very delicate branch coming from the optocœl and joining Reissner's fibre as it emerges from the sub-commissural canal.

The only real addition to our knowledge of Reissner's fibre made by Ayers is contained in his statement that the ultimate fibrillæ are derived from the cells of the ependymal epithelium. Unfortunately great importance cannot be attached to his account, for it is far from certain that much which he has interpreted as "ventricular fibre" is not really coagulum. In *Petromyzon*, both in larvæ and adults, he states that he was unable to find these fibres. In their place he found "a fine-meshed network of fibrils . . . which bears the same relations to the ependymal cells and in life practically fills the ventricular cavity." In this case there can be no doubt, from his description, that he refers to the fibre-like coagulum which commonly occurs in the brain-ventricles, and has altogether overlooked Reissner's fibre.

He suggests that the function of these fibrillæ is to bring

the ependymal epithelial cells into intimate connection, and that they are possibly in some way connected with the control of the lymph supply in the ventricles.

Holm makes no reference to the occurrence of Reissner's fibre, although he seems to have seen the isthmic canal, of which in *Myxine* it may be said that it has persisted merely because it gives free passage to that structure. In the case which he describes ('01, p. 369) the isthmic canal (his "upper canal") was evidently much less reduced than is commonly the case.

He has apparently followed Retzius ('94) in his erroneous identification of the ventricle of the mid-brain as the fourth ventricle. As I have pointed out above, the cavity of the mid-brain is greatly reduced, its anterior portion being represented only by the sub-commissural canal, while the whole of that large space (optocœl), which in the *Petromyzontidæ* (Text-fig. 5) lies above and behind the posterior commissure in the roof of the mid-brain, is reduced in *Bdellostoma* (Text-fig. 7) to a more or less complete annular space, and in *Myxine* (Text-fig. 8) to a short, dorsally directed and blindly ending canal. Behind, beneath the posterior portion of the corpora bigemina, the aqueductus Sylvii is, in the *Myxinioids*, reduced to two narrow passages, the isthmic and ventricular canals.

The main cavity, then, in the mid-brain ventricle, which, with the ventricular canal, is identified by Sanders,<sup>1</sup> Holm

<sup>1</sup> In justice to Sanders, whose work appears to have been largely overlooked, it should be pointed out that his observations were really remarkably correct, and that in many particulars he has anticipated the results of more recent workers. Not only did he identify correctly nearly all of the various brain-ventricles, but later work has also justified his identifications of various parts of the brain. He continued the observations of Retzius as to the absence of a cerebellum. Curiously enough, Holm ('01, p. 378) misrepresents Sanders as interpreting the corpora bigemina as the cerebellum, a mistake which, in view of Sanders actual statements, is altogether inexplicable. Thus ('94, p. 6), Sanders says, "It is remarkable that the cerebellum . . . is here entirely absent," and again (op. cit., p. 22), "*Myxine* appears to present



and Ayers as the fourth ventricle, represents actually but a small portion of the aqueductus Sylvii, and I have preferred, for that reason, to speak of it as the sinus mesocœlicus.

Sterzi ('07) identifies it correctly as the cavity of the mid-brain, he appears not to have noticed the isthmic canal in Myxine, although he saw and called attention (op. cit., p. 539) to the occurrence of small scattered spaces that continue backwards from it towards the upper canal of the spinal cord. He, so far as I can find, makes no reference whatever to the occurrence of Reissner's fibre.

Sargent ('04) quotes that part of Sanders' descriptions which relates to the course of Reissner's fibre in the brain, and dismisses it without further comment. He also quotes without comment the preceding paragraph, in which Sanders describes the ending of the fibre posteriorly, and, as above stated, he dismisses Studnička's statements which confirmed those of Sanders, remarking that the appearances so interpreted by Studnička must be due to the disturbed and abnormal condition of the fibre in his preparations.

Sargent's only other statement which bears upon the condition of the fibre in Myxinoids is the wholly unwarranted assumption ('04, p. 162) that "In Myxine, which is blind . . . Reissner's fibre must be made up wholly of axons from the olfactory centre in the ganglion habenulæ."

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the only instance in the vertebrate kingdom of the entire absence of an important section of the brain, viz. the cerebellum." It was Sanders, too, who first pointed out the existence of the terminal sinus in Myxine. Retzius to whom is commonly attributed the discovery of this terminal dilatation of the spinal cord, to which he gave the name of the terminal sinus, only published in the following year. Sanders' description of the condition of the hinder end of the canalis centralis of the spinal cord anticipated Sterzi's by more than a dozen years.

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## EXPLANATION OF PLATES 1-5,

Illustrating Prof. George E. Nicholls' paper on "The Structure and Development of Reissner's Fibre and the Sub-commissural Organ."—Part I.

## LIST OF REFERENCE LETTERS.

*c. bg.* Corpora bigemina. *c. c.* Canalis centralis of the spinal cord. *c. c.'* Upper canal of canalis centralis (in Myxinoids). *cil.* Cilia. *Dk.* Cells of the "Dachkern." *e. ep.* Ependymal epithelium. *ep.* Epiphysis. *fb., fb.'* Fibrillæ of Reissner's fibre. *h. g.* Habenular ganglion. *i. c.* Isthmic canal. *inf.* Recessus infrapinealis. *iter.* Iter. *mng.* Meninges. *m. r.* Mesocœlic recess. *m. t.* Cells of the terminal mass. *nch.* Notochord. *n. p. c.* Nucleus of the posterior commissure. *op.* Optocœl; optocœlic canal (Myxinoids). *op.'* Posterior extension of optocœlic canal. *p. c.* Posterior commissure. *r. d.* Dialectic recess. *r. f.* Reissner's fibre. *r. f.'* Reissner's fibre, tangled in canalis centralis. *r. f.{'* Reissner's fibre, tangled in sinus terminalis. *s. c.* Spinal cord. *s. c. c.* Sub-commissural canal. *s. c. o.* Sub-commissural organ. *s. m.* Sinus mesocœlicus. *s. m.'* Upper chamber of sinus mesocœlicus. *s. m.{'* Lower chamber of sinus mesocœlicus. *s. t.* Sinus terminalis. *t. c.* Tela choroidea II. *tect. mes.* Tectum mesencephali. *t. p.* Terminal plug. *v. c.* Ventricular canal. *x.* Large space (part of fourth ventricle) in roof of hind-brain, lying above the canal-like fourth ventricle. III. Third ventricle. IV. Fourth ventricle. \* Indicates the position of the extremity of the notochord in Fig. 52.

[Figs. 1-32 are all reproduced from photomicrographs; the remaining figures, 33-58, were drawn from the actual preparations with the aid of a camera lucida.]

## PLATE 1.

Figs. 1-9 represent the sub-commissural organ of typical members of the different vertebrate sub-classes, as seen in transverse sections of the brain.

Fig. 1.—*Petromyzon fluviatilis*. × 28.

Fig. 2.—*Raia blanda*. × 65.

Fig. 3.—*Scyllium canicula*. × 24.



Fig. 4.—*Esox lucius*.  $\times 28$ .

Fig. 5.—*Rana temporaria*.  $\times 128$ .

Fig. 6.—*Sphenodon* (Hatteria) *punctatus*.  $\times 24$ .

Fig. 7.—*Gallus domesticus* (19-day chick).  $\times 24$ .

Fig. 8.—*Microtus arvensis*.  $\times 52$ .

Fig. 9.—*Lepus cuniculus*.  $\times 24$ .

## PLATE 2.

Fig. 10.—*Petromyzon fluviatilis*. Part of a transverse section through the hinder part of the mid-brain, showing the paired condition of the isthmic canal.  $\times 320$ .

Fig. 11.—*P. fluviatilis*. Part of a horizontal section through the same region of the brain, showing the junction of the right and left factors of Reissner's fibre at a point just anterior to the isthmic canal (here median and not visibly a paired structure).  $\times 340$ .

Fig. 12.—*P. fluviatilis*. Part of a median sagittal section through the end of the spinal cord showing the *canalis centralis* expanding into a *sinus terminalis*, within which is seen a tangled mass of Reissner's fibre, lying against the meningeal wall.  $\times 250$ .

Fig. 13.—*P. fluviatilis*. A similar section (but slightly oblique) through the *sinus terminalis* of another specimen. Reissner's fibre is inserted into the meningeal sheath of the sinus.  $\times 250$ .

Fig. 14.—*Ichthyomyzon* (*Entosphenus*) *tridentatus*. A sagittal section through the tail of an ammocete of 105 mm. showing the *sinus terminalis* and Reissner's fibre.  $\times 80$ .

Fig. 15.—*I. tridentatus*. Part of a sagittal section through the tail of an ammocete of 90 mm. showing a considerable tangle of Reissner's fibre almost filling the *sinus terminalis*.  $\times 350$ .

Fig. 16.—*Petromyzon fluviatilis*. Part of a sagittal section through the spinal cord showing the interrupted coiling of Reissner's fibre.  $\times 600$ .

Fig. 17.—*Myxine glutinosa*.—Sagittal section through the *sinus terminalis*, showing a large mass of coiled Reissner's fibre. At the apex of the mass the fibre is more loosely looped.  $\times 260$ .

Fig. 18.—*M. glutinosa*. Another section from the same series as fig. 17, passing almost centrally through the mass of fibre.  $\times 260$ .

Fig. 19.—*Geotria australis*. Part of a median sagittal section through the posterior commissure, showing a tangle of Reissner's fibre below the sub-commissural organ (from one of Prof. Dendy's preparations).  $\times 310$ .

Fig. 20.—*G. australis*. Part of a median sagittal section through the hind-brain (from one of Prof. Dendy's preparations). A great length of Reissner's fibre is seen lying in the fourth ventricle and canalis centralis (somewhat displaced).  $\times 150$ .

## PLATE 3.

Fig. 21.—*Bdellostoma* (*Polistotrema*) *stouti*. Part of a median sagittal section through the mid-brain.  $\times 50$ .

Fig. 22.—*B. stouti*. Part of a nearly median sagittal section through the mid-brain of another specimen, showing the optocœl much more reduced. Reissner's fibre is seen issuing from the sub-commissural canal.  $\times 60$ .

Figs. 23–25.—*B. stouti*. Portions of transverse sections through the mid-brain of another specimen. These are taken approximately at the levels indicated by the lines 23, 24, 25 in Text-fig. 7.  $\times 68$ .

Figs. 26, 27.—*Myxine glutinosa*. Portions of transverse sections through the mid-brain, corresponding roughly to those shown for *Bdellostoma* in figs. 23, 25. The cavities in *Myxine* are, however, relatively much smaller. Fig. 26  $\times 115$ . Fig. 27  $\times 200$ .

Fig. 28.—*M. glutinosa*. Part of a transverse section through the spinal cord, showing the double character of the canalis centralis and Reissner's fibre in the lower of the two canals.  $\times 350$ .

Fig. 29.—*M. glutinosa*. Part of a sagittal section through the spinal cord.  $\times 60$ .

Fig. 30.—*M. glutinosa*.—Part of a sagittal section through the hind-brain and spinal cord, showing the large space (*x*) situated in the hind-brain above the canal-like portion of the fourth ventricle.  $\times 150$ .

Fig. 31.—*Bdellostoma stouti*. Part of a transverse section through the spinal cord for comparison with that of *Myxine* (fig. 28).  $\times 450$ .

Fig. 32.—*B. stouti*. Part of a sagittal section through the spinal cord showing Reissner's fibre in the lower canal.  $\times 68$ .

## PLATE 4.

Fig. 33.—*Petromyzon fluviatilis*. Part of a transverse section through the thalamencephalon, showing the sub-commissural organ (on the true left side) between the right habenular ganglion and the left optic thalamus.  $\times 30$ .

Fig. 34.—*P. fluviatilis*. Part of another transverse section, taken at a point immediately anterior to the posterior commissure.  $\times 30$ .

Fig. 35.—*P. fluviatilis*. Part of another transverse section, through the posterior commissure, showing the right diacelic recess.  $\times 30$ .

Fig. 36.—*P. fluviatilis*. Another transverse section through the mid-brain, immediately behind the posterior commissure, showing the end of the sub-commissural organ.  $\times 30$ .

Fig. 37.—*P. fluviatilis*. Horizontal section through the sub-commissural organ, showing the paired character of Reissner's fibre. (Some of the lesser branches were added from adjacent sections.)  $\times 240$ .

Fig. 38.—*P. fluviatilis*.—Part of a transverse section through the posterior commissure, showing the sub-commissural organ and Reissner's fibre, cut obliquely, lying closely against it on each side.  $\times 240$ .

Fig. 39.—*P. fluviatilis*. Part of a horizontal section through the sub-commissural organ anterior to the posterior commissure, showing the fibrillæ of Reissner's fibre arising from the surface of the organ.  $\times 525$ .

Fig. 40.—*P. fluviatilis*. Median section through the extremity of the filum terminale, showing the canalis centralis opening widely by the terminal neural pore in the sinus terminalis. (The figure was obtained by the superposition of drawings of several adjacent sections which were cut slightly obliquely to the sagittal plane.)  $\times 160$ .

Fig. 41.—*Ichthyomyzon (Entosphenus) tridentatus*. A transverse section through the developing sub-commissural organ of an ammocete 12 mm. long. (The level of the section is indicated by the line 41 in fig. 45.)  $\times 560$ .

Fig. 42.—*I. tridentatus*. A transverse section through the sub-commissural organ of an ammocete 40 mm. long. The level of the section is approximately indicated by the line 42 in fig. 46.)  $\times 320$ .

Fig. 43.—*I. tridentatus*. A transverse section through the sub-commissural organ of an ammocete 95 mm. long.  $\times 300$ .

Fig. 44.—*I. tridentatus*.—Part of a transverse section through the hinder part of the mid-brain of an ammocete, 65 mm. long, showing the paired character of the isthmie canal.

#### PLATE 5.

Fig. 45.—*Ichthyomyzon tridentatus*. Part of a sagittal section through the roof of the brain of an ammocete 145 mm. long, showing the extent of the posterior commissure and the sub-commissural organ.  $\times 525$ .

Fig. 46.—*I. tridentatus*. Part of a sagittal section through the roof of the brain of an ammocete 30 mm. long.  $\times 320$ .

Fig. 47.—*I. tridentatus*. Transverse section through the tail of an ammocete 12 mm. long, showing the condition of the *canalis centralis*.  $\times 420$ .

Fig. 48.—*I. tridentatus*. A similar section through the tail of the same ammocete, taken at a point 40 micra behind that represented in fig. 47.  $\times 420$ .

Fig. 49.—*I. tridentatus*. Another section from the same series, taken at a point 50 micra posterior to that shown in fig. 48, and distant only 20 micra from the actual end of the tail. It shows the *canalis centralis* widened out into a *sinus terminalis*.  $\times 420$ .

Fig. 50.—*I. tridentatus*. A median sagittal section through the tail of an ammocete 14.5 mm. long, showing Reissner's fibre ending in a terminal plug in the *sinus terminalis*.  $\times 518$ .

Fig. 51.—*I. tridentatus*. Median sagittal section through the tail of an ammocete 42 mm. long, showing Reissner's fibre expanded into a terminal plug inserted into the wall of the *sinus terminalis*.  $\times 394$ .

Fig. 52.—*I. tridentatus*. A similar sagittal section through the end of the tail of an ammocete 75 mm. long, showing Reissner's fibre coiled in the *sinus terminalis*.  $\times 394$ .

Fig. 53.—*I. tridentatus*. A section cut somewhat obliquely to the sagittal plane, showing Reissner's fibre ending in a terminal plug in the *sinus terminalis* of an ammocete 36 mm. long.  $\times 690$ .

Fig. 54.—*I. tridentatus*. A sagittal section through the tail of an ammocete 105 mm. long. (Reissner's fibre has been completed from one or two adjoining sections.)  $\times 94$ .

Fig. 55.—*I. tridentatus*. A nearly transverse section through the anterior part of the *sinus terminalis* of an ammocete 65 mm. long. Reissner's fibre has retracted into a coil, and some fibrous tissue appears to have been pulled into the *sinus terminalis*.  $\times 560$ .

Fig. 56.—*I. tridentatus*. A sagittal section through part of the spinal cord of an ammocete 34 mm. long.  $\times 560$ .

Fig. 57.—*Geotria australis*. Part of a sagittal section through the mid-brain of a velasia stage showing the pair of principal factors of Reissner's fibre uniting about halfway between the sub-commissural organ and the isthmus canal.  $\times 105$ .

Fig. 58.—*G. australis*. A sagittal section through the posterior commissure of another velasia, showing Reissner's fibre broken and retracted slightly forwards. (From one of Prof. Dendy's preparations.)  $\times 104$ .